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JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Conducted and published for the Club, by

ALBION REED HODGDON, Editor-in-Chief

ALBERT FREDERICK HILL
RALPH CARLETON BEAN
ROBERT CRICHTON FOSTER
ROLLA MILTON TRYON
RADCLIFFE BARNES PIKE
ELIZABETH ANNE SHAW
} Associate Editors

VOLUME 73

1971

The New England Botanical Club, Inc.

Botanical Museum, Oxford St., Cambridge 38, Mass.

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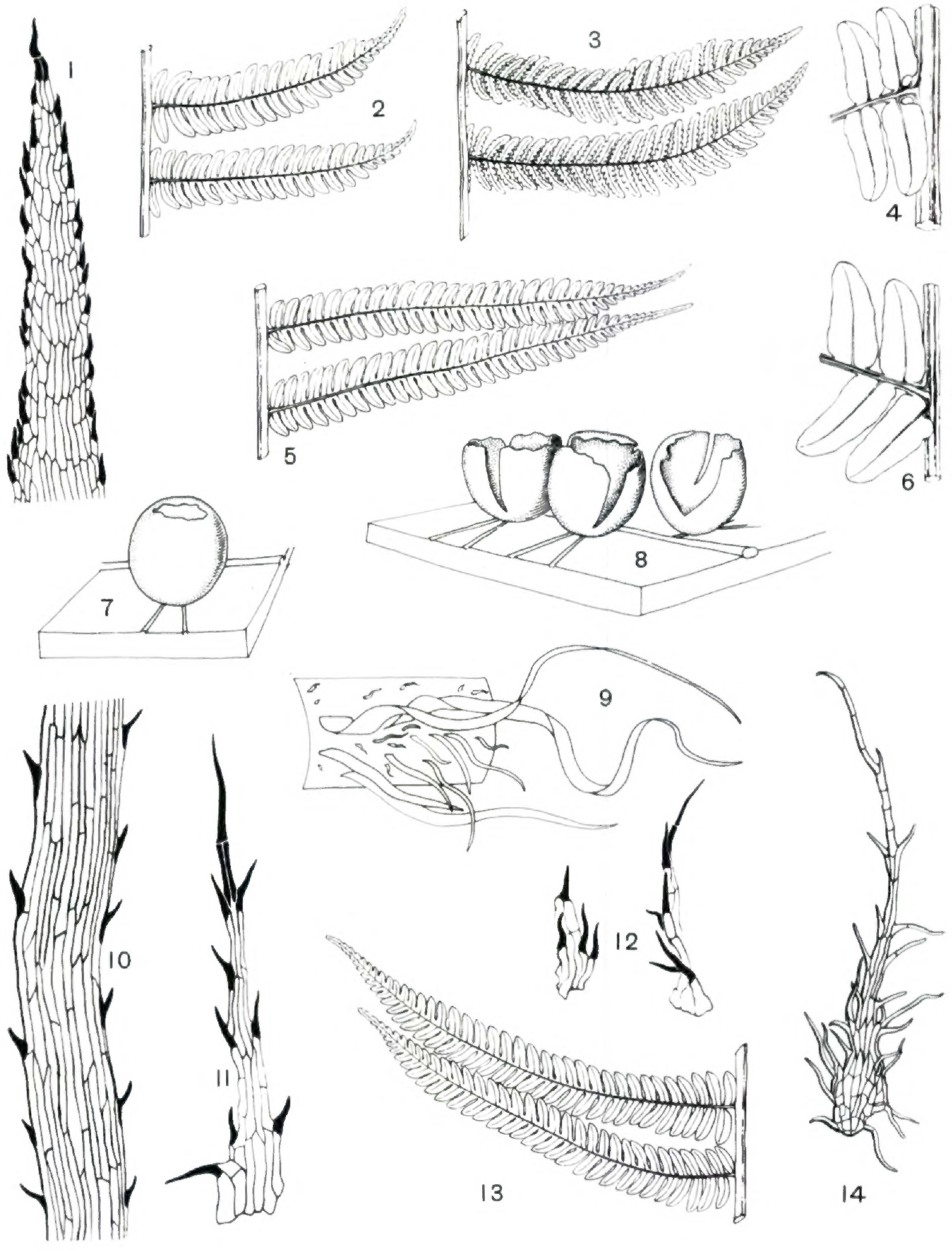
THE AMERICAN TREE FERNS ALLIED TO SPHAEROPTERIS HORRIDA

ROLLA TRYON

The genus *Sphaeropteris* of the Cyatheaceae contains about 120 species, most of them growing in the paleotropics from India and southeastern Asia eastward through the Pacific to Pitcairn Island. Holttum (1963, 1964, 1965) has treated these as *Cyathea* subgenus *Sphaeropteris*. The few American species, perhaps twenty in number, have never been dealt with as a group, nor until recently have their generic relations been satisfactorily known. In my treatment of the genera of the Cyatheaceae (Tryon, 1970) the subgenus *Sphaeropteris* of Holttum was recognized as a genus and slightly enlarged to include related American species that were not entirely like any of those of the paleotropics. The present revision is concerned with the only American element of the genus that does have clear relations to species of the paleotropics. This is a small group of species allied to *Sphaeropteris horrida (Cyathea princeps)*. The relation of the *Sphaeropteris horrida* group to species such as *Sphaeropteris medullaris* of New Zealand and *S. concinna* of New Guinea is so close that it must be accepted as a true (evolutionary) neotropic-paleotropic relationship. The group of *Sphaeropteris horrida* is a closely knit one of six species. It is readily distinguished from other groups and species among the American members of



Figs 1-4. *Sphaeropteris insignis*. 1. Apical portion of crozier scale, Jamaica, *Riba* 211, GH, × 32. 2. Central fertile pinnules of the usual form, Jamaica, *Maxon* 1463, US, × 0.4. 3. Central fertile pinnules of the form with lobed tertiary segments, Jamaica, *Riba* 211, GH, × 0.4. 4. Base of pinnule, Cuba, *Hioram* 7021, GH, (enlarged).

Figs. 5-8. *Sphaeropteris horrida*. 5. Central fertile pinnules, Guatemala, *Steyermark* 33432, US, × 0.4. 6. Base of pinnule, Mexico, *Purpus* 9197, GH (enlarged). 7. Immature indusium (somewhat dia-

the genus by the complete indusium that is a deep cup or urn or completely encloses the sorus. The other American species either lack an indusium or have a partially developed (hemitelioid) one. The following description provides a detailed summary of the characteristics of the group.

Stems up to 5- (in *S. horrida*) 15 m. tall and 15- (in *S. horrida*) 40 cm. in diameter, with more or less persistent scales similar to those of the petiole; leaf (in *S. Gardneri*) often 1, usually 2-3, or (in *S. horrida*) to 5 m. long; petiole usually thick, sometimes massive, ca. 30-100 cm. long, lacking spines, rather smooth except in *S. insignis* and *S. horrida* in which it may be muricate from the persistent scale bases; indument varied, represented by minute scales (squamulae) (these sometimes mixed with minute trichomes) that may intergrade with large, elongate scales to ca. 4 cm. long (Fig. 9), these of nearly uniform cellular construction (structurally conform) and with dark marginal teeth that are rather regular in their size, spacing and orientation (Fig. 10), the scales persistent basally or (in *S. Brunei* and *S. Cuatrecasaii*) often long-persistent along the whole petiole; lamina mostly bipinnate-pinnatifid to bipinnate-pinnatisect, rarely a portion tripinate-pinnatifid, the lower pinnae petiolulate, usually strongly so; pinnules with the basal segments excavated and sometimes auriculate, light colored (usually whitish) beneath partly from the glaucous surface and (perhaps) partly from the structure of the stomata guard cells; ultimate segments with scales and (or) trichomes, these more abundant on the abaxial surface of the fertile than the sterile segments

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grammatic), Guatemala, *Wilson* 218, F × 8. 8, Mature indusia (somewhat diagrammatic, receptacle not shown), same as 7.

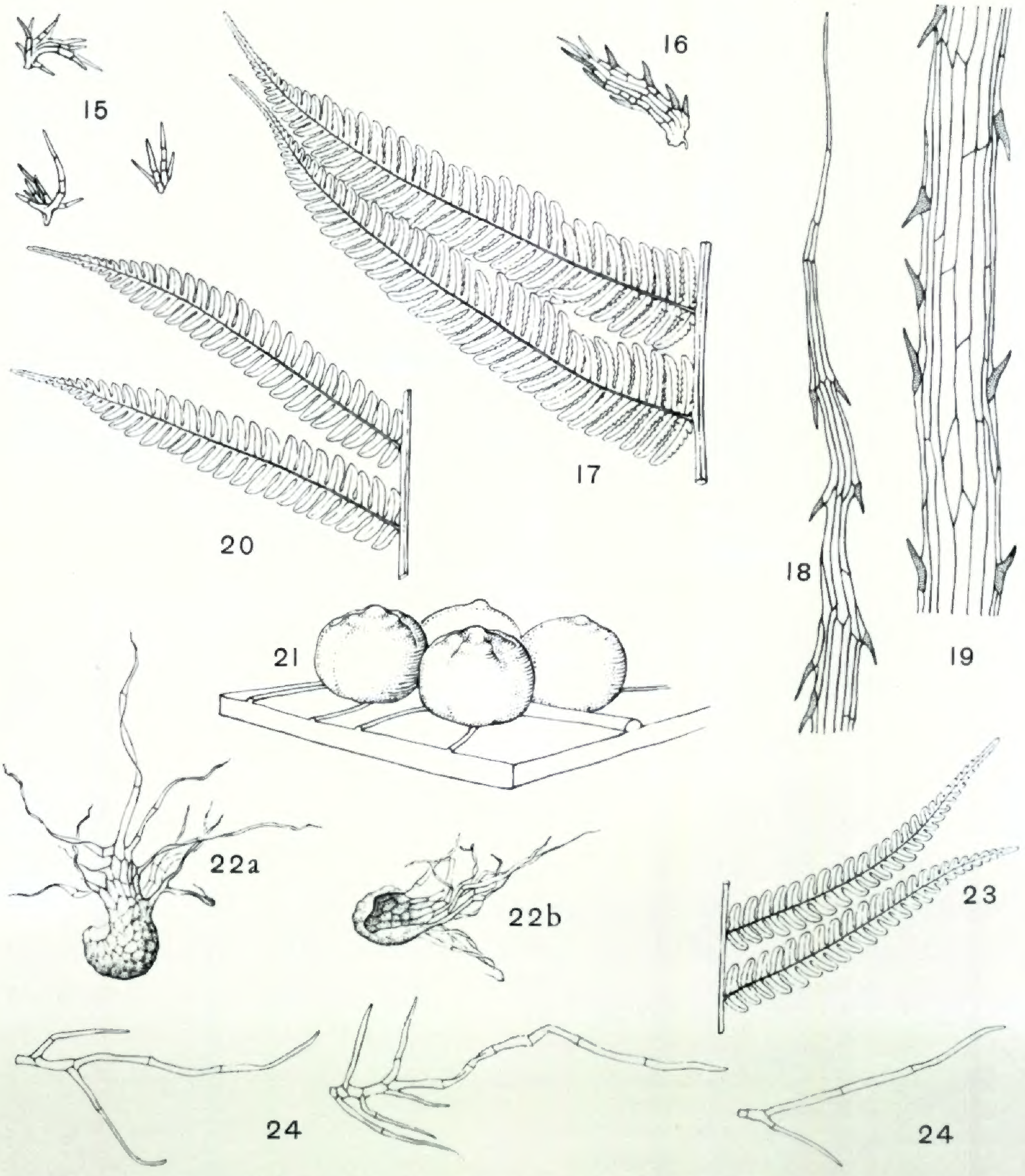
Figs. 9-14. *Sphaeropteris Brunei*. 9. Diagram of petiole surface with scales, Costa Rica, *Nisman* 114, GH (enlarged). 10. Central portion of large petiole scale, same as 9, × 32. 11. Small petiole scale, same as 9, × 32. 12. Squamulae of petiole, same as 9, × 32. 13. Central fertile pinnules, Costa Rica, *Gastony* 795 GH, × 0.4. 14. Scale of costule (beneath), Costa Rica, *Scamman & Holdridge* 7859, GH, × 32.

where they may be sparse or rarely nearly lacking, the adaxial surface glabrous or rarely with a few trichomes, the veins usually 1-forked, less often simple or 2-forked; indusium usually firm, brown or light-tan and opaque, with a minutely roughened suface, sometimes thinner and sub-opaque, rarely translucent, cyatheoid (a deep cup, Fig. 7) to sphaeropteroid (globose, Fig. 21); the sorus borne at the fork of the fertile vein, receptacle tall, more or less clavate, paraphyses numerous, long, with an enlarged apex; spores tetrahedral-globose, brownish, rather delicately (at ca. 400 ×) marked with low, usually close ridges with sharp prominences.

Juvenile plants of *Sphaeropteris horrida* and *S. Brunei* differ from adult ones (in addition to the expected characters of stem and leaf size, complexity of the lamina and a decumbent stem) by having a few large stout trichomes borne toward the apex of the ultimate segments on the adaxial surface and in having the indument of the lamina sparingly, if at all developed.

The species of the *Sphaeropteris horrida* group grow in forests, in wooded ravines and at forest borders in humid mountainous regions from ca. 600 to 2700 m. The distribution of the species (Map A) is from Hispaniola, Jamaica and Cuba to Mexico and Panama, Colombia to Bolivia and southeastern Brazil. This is a basic Cordilleran pattern of distribution that frequently occurs in plants, especially in a group of related species. Sometimes the pattern is more extensive with extensions into Puerto Rico and Venezuela, while in other examples it may be limited to the Andes and Central America.

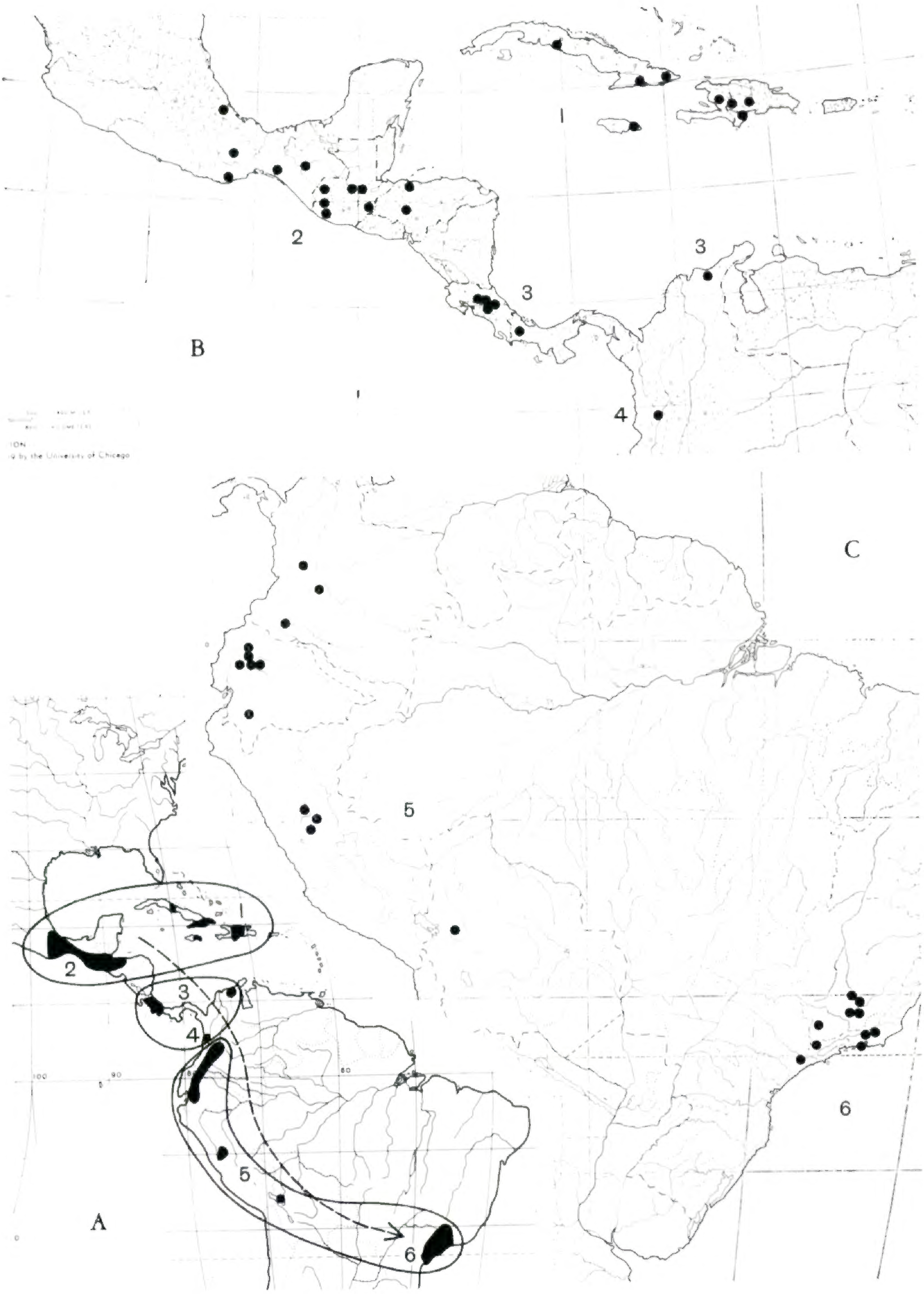
All of the species that are represented by a considerable number of collections exhibit significant variation and this is discussed especially in *Sphaeropteris Brunei* and *S. quindiuensis*. This variation may extend to the diagnostic characters, as in *Sphaeropteris insignis* and *S. horrida* where no single character is always distinctive, or as in *Sphaeropteris quindiuensis* and *S. Gardneri* where the characteristic indument of each species varies considerably in its abundance.



Figs. 15-17. *Sphaeropteris Cuatrecasasii.* 15. Squamulae of petiole, uniform dark color not indicated. Colombia, *Cuatrecasas* 22423, US, × 32. 16. Small petiole scale, same as 15. 17. Central fertile pinnules, same as 15 but F, × 0.4

Figs. 18-22. *Sphaeropteris quindiuensis.* 18. Apex of crozier scale, Ecuador, *Sparre* 16337, GH, × 32. 19. Same as 18 but below apex, showing transition from retrorse to antrorse teeth. 20. Central sterile pinnules, Ecuador, *Sparre* 16337, GH, × 0.4. 21. Immature indusium (somewhat diagrammatic), Ecuador, *Sparre* 16871, GH, × 8. 22. Bullate scales of the costule (beneath) — a) upper view, b) under view, Colombia, *Schultes & Villarreal* 7711, GH, × 32.

Figs. 23-24. *Sphaeropteris Gardneri.* Central fertile pinnules, Brazil, *Widgren* in 1844, GH, × 0.4. 24. Branched trichomes of costule and veins (beneath), Brazil, *Macedo* 2883, MO, × 32.



Map A. Distribution of the *Sphaeropteris horrida* group: species (in black), numbered as in Maps B and C, closely related species enclosed by an ellipse, arrow indicates proposed direction of phyletic advance and migration route of the group. Map B. Distribution of 1. *Sphaeropteris insignis*, 2. *S. horrida*, 3. *S. Brunei*, 4. *S. Cuatrecasasii*. Map C. Distribution of 5. *Sphaeropteris quindiuensis*, 6. *S. Gardneri*.

It is clear that the species have not yet evolved into highly distinctive taxa. I have chosen to treat them all as species because the present materials are neither extensive nor always complete and they do not provide an adequate basis for a more refined taxonomic interpretation of the taxa.

Sphaeropteris insignis and *S. horrida* may be considered as the most primitive species in the group on the basis of their open indusium (which also is sometimes deeply cleft) and their crozier scales which bear wholly antrorse teeth. The four other species are advanced with a fully closed (sphaeropteroid) indusium and with the scales borne at the top of the crozier with retrorse teeth apically. Among these species *S. Gardneri*, with a strong development of simple or branched trichomes on the abaxial surface of the ultimate segments, and *S. quindiuensis* with bullate scales on the costule, beneath, seem to be more specialized. *Sphaeropteris Brunei* and *S. Cuatrecasasii*, then, occupy an intermediate phyletic position. The species also find their closest relations at these phyletic levels so that they may be grouped into three pairs and arranged as follows: *S. insignis-S. horrida, S. Brunei-S. Cuatrecasasii* and *S. quindiuensis-S. Gardneri.*

The strong correlation of phyletic level and species relations suggests that the evolution and speciation are fully displayed in this group. As mentioned above, the species are not very strong ones so that there are no major gaps between them that might obscure their evolutionary history. The correlation of this history with the geography of the species indicates that geographic speciation has had a decisive role in the development of the group. This is illustrated in Map A where the related pairs of species are enclosed in ellipses and the correlated directions of phyletic advance and of migration is indicated.

Key to species

a. Indusium usually a deep cup to a deep urn (Fig. 7) (it may appear as sphaeropteroid when immature, but no apical umbo is present), splitting at maturity into 2-few segments (Fig. 8); or sometimes, especially the basal

indusia (and more often in *S. insignis*), narrowly to widely cleft on the side toward the margin of the segment, the margins of the indusium usually irregularly crenulate or ciliate; marginal teeth on the scales that are borne at the top of the fully coiled crozier all antrorse to patent (Fig. 1). b.

b. Petiole scales that are ca. 5 mm. long broadest well above the base; central pinnules of the central pinnae with the basiscopic costule arising from the costa or its expanded base (Fig. 4); segments of the split indusium irregularly disposed; Cuba, Jamaica, Hispaniola .... 1. *S. insignis.*

b. Petiole scales that are ca. 5 m. long broadest at or near the base; central pinnules of the central pinnae with the basal basiscopic costule arising from the pinna-rachis (Fig. 6); segments of the split indusium nearly maintaining its original form (Fig. 8); Mexico, Guatemala, Honduras ...... 2. *S. horrida.*

a. Indusium sphaeropteroid, with an apical umbo (Fig. 21), splitting at maturity into 2-few segments, one of them retaining the umbo; marginal teeth at the apex of some of the scales that are borne at the top of the fully coiled crozier retrorse (Fig. 18), changing to antrorse below (Fig. 19). c.

c. Costules bearing trichomes (Fig. 24) or flattened scales (Fig. 14) beneath, no bullate scales present. d.

d. Costules bearing flattened scales beneath and also sometimes simple or branched trichomes, the scales predominent unless the indument is sparse and then they may be few or lacking. e.

e. Squamulae on the surface of the petiole (usually best seen beneath the persistent large scales) few to many, approximate to scattered, most with a definite body and marginal setae (Fig. 12); scales of the costule, beneath, mostly light colored basally and darker apically, or concolorous, usually with dark cilia; Costa Rica, Panama, northern

Colombia .... *S. Brunei.*

e. Most squamulae on the surface of the petiole (usually best seen beneath the persistent large scales) minute, these forming a dense layer, substellately highly dissected into few arms (Fig. 15); scales of the costule, beneath, mostly dark colored basally and lighter apically, with light colored cilia; central Colombia .. .. 4. *S. Cuatrecasasii.*

d. Costule bearing numerous simple or branched trichomes beneath (Fig. 24), rarely a few flattened scales also present; southeastern Brazil .. .. 6. *S. Gardneri.*

c. Costules bearing some to many bullate scales beneath (Fig. 22), especially on fertile segments, rarely they may be absent on sterile segments, flattened scales or simple or branched trichomes may also be present; Colombia to Bolivia ... 5. *S. quinduiensis.*

1. **Sphaeropteris insignis** (D. C. Eaton) Tryon, Contrib. Gray Herb. 200: 20. 1970. Map B. Figs. 1-4.

Cyathea insignis D. C. Eaton, Mem. Amer. Acad. n.s. 8: 215. 1860. Holotype: La Guinea, eastern Cuba, Dec. 15, 1859, *Wright* 1064 YU. Isotypes (lacking locality and date): B! GH! MO! NY! P!

Cyathea moniliformis Jenm. (as *moniliforme*) Bull. Misc. Inform. Roy. Bot. Gard. Trinidad no. 15 (vol. 3, part 7): 59. 1898. Holotype: without collector or locality, I consider it to have been collected in Jamaica. Isotype or part of the Holotype: Botanic Gardens Herbarium (Trinidad), "no. 17, *Alsophila armata* Presl," TRIN!, photo and fragment, BM! photo GH; "Trinidad, W. Indies," Herb. Jenman, NY! photo GH.

Sphaeropteris insignis usually differs in several characters from the closely related *S. horrida.* However, all of these are variable and the range of variation in one species may overlap with that in the other. In addition to the differences mentioned in the key, the leaves of *S. insignis* are often smaller than those of *S. horrida,* the central pinnae

may be more elongate and the fertile segments are sometimes contracted and lobed (Fig. 3).

The apparently distinctive characters of *Cyathea moniliformis* — the prominent rounded lobes of the tertiary segments with strongly recurved margins, the strongly muricate pinna-rachises and the scales of the abaxial surface of the costules which have a whitish body and are strongly dissected into usually dark arms — are all present (although sometimes rare and not always as extreme) among the material I have examined of *Sphaeropteris insignis*. The spores of the two are alike. I believe that the provenance of the type specimen of *Cyathea moniliformis* was Jamaica and that it represents a variation of *Sphaeropteris insignis*. Figure 3 represents a specimen of *S. insignis* with lobed pinnules similar to those in *Cyathea moniliformis*.

The original description of *Cyathea moniliformis* includes characters of the size and disposition of the leaf that could not have been obtained from the type material cited above. The sheet at TRIN bears the apical portion of a pinna and at NY a central portion (perhaps of the same pinna); there are no notes with either sheet. This implies that Jenman had other materials and since these, if extant, might qualify as the holotype, the technical status of the specimens cited as types is in doubt.

Sphaeropteris insignis grows in the moist mountainous regions of Hispaniola, Jamaica and Cuba at ca. 750-1800 m. Additional specimens seen:

Cuba. LAS VILLAS (formerly Santa Clara): Buenos Aires, Trinidad Mts., *Hodge & Howard* 5242 (A), *León et al.* 14024, 14025, 14026 (NY), *Jack* 7271 (F, GH), *Morton* 4161 (GH, MO, NY, P, US); Sliguanéa, Trinidad Mts., *Ekman* 18516 (NY); Aguacate, Trinidad Mts., *Britton & Wilson* 5369 (NY, P). ORIENTE: El Cobre, Loma del Gato, Sierra Maestra, *Clèment* 1673 (US); Loma del Gato, *Hioram* 7021 (GH); Loma San Juan, *Hioram* 7310 (US). **Jamaica.** *Gilbert* 79 (NY); *A. Moore* in 1897 (MO); *Jenman* (NY). ST. ANDREW: Monkey Hill, above New Haven Gap, *Maxon* 2700 (US); above New Haven Gap, *Underwood* 3221 (NY, P); Moody's Gap, *Underwood* 1587, 2153 (NY). PORTLAND: St. Georges, *Jenman* (NY); Road to St. Georges, *Harris* 7622 (F), (probably *Harris*) 7722 (NY); Hardwar Gap and vicinity,

ca. 3/4ths mile south (air) of Green Hill, *Riba* 211 (GH, MEXU). ST. THOMAS: Portland Gap, *Underwood* 1443, 2478 (NY), *Maxon* 1463 (US). HISPANIOLA. **Haiti:** Morne la Selle, *Holdridge* 1968 (NY, US); Bazil, Morne Sal, *Cook* 32 (GH, US). **Dominican Republic:** LA VEGA: Constanza, *Ekman* H13891 (B, F, GH, NY); Constanza to Valle Nuevo, *Gastony et al.* 732 (GH, NY). SAN RAFAEL: Sierra de Neiba, near Haiti border, *Gastony et al.* 434 (GH, NY). BARAHONA: Noche Buena Berg, *Fuertes* 1058 (F, GH, MO, NY, P, US).

2. **Sphaeropteris horrida** (Liebm.) Tryon, Contrib. Gray Herb. 200: 20. 1970. Map B. Figs. 5-8.

Cibotium horridum Liebm. Vid. Selsk. Skr. V, 1: 279. 1849. Lectotype: Teotalcingo, Chinantla, Oaxaca, Mexico, 4-5000 ft. *Liebmann* 873 (Mex. Pl. 2086) Fol. Herb. C!, photo GH, US, fragment US! Paratype: Inter Trapide de la Concepción et Totontepec, Oaxaca, Mexico, 4-4500 ft., *Liebmann* (Mex. Pl. 2102) Fol. Herb. C! Not *Cyathea horrida* (L.) J. E. Sm. Mém. Acad. Turin 5: 416. 1793.

Cibotium princeps Linden ex. J. Sm. Ferns Brit. & For. 291. 1866, in synon.

Cyathea princeps J. Sm. Ferns Brit. & For. 291. 1866, nomen nudum.

Cyathea princeps E. Mayer, Gartenfl. 17: 10. 1868. Syntypes: Cult. Linden (Brussels) ex Volcán Tuxetla, Veracruz and Chiapas, Mexico. Authentic material has not been seen but there seems to be no doubt about the correct application of the name, providing that the material mentioned by Mayer from Costa Rica (probably representing *Sphaeropteris Brunei*) is excluded. Cultivated material identified as *Cyathea princeps* and dating from the decade of 1860 is accurately named.

Cyathea Bourgaei Fourn. Mex. Pl. 1: 135. 1872. Lectotype: Valle de Córdoba, Mexico, *Bourgeau* 2200. Isotypes: GH! NY! P! (several sheets but none from Herb. Fournier). The Bolivia collection, *Weddell* 4567 P! also cited by Fournier, is to be excluded.

Cyathea glauca Fourn. Mex. Pl. 1: 135. 1872, not Willd. Sp. Pl. 5: 493. 1810. Holotype: Orizaba, Mexico, *Bourgeau* 2794. Specimens of this number are commonly *Nephelea mexicana (Cyathea mexicana)* (P, GH, NY) but some are

Sphaeropteris horrida (P). I did not find this collection in Herb. Fournier at Paris (1969) and consequently there is uncertainty as to the identity of the original material. The description seems to indicate that *S. horrida* was the principal, or only, element included.

Cyathea Munchii Christ, Bull. Herb. Boiss. II, 7: 413. 1907. Syntypes: San Cristóbal, Chiapas, Mexico, *Münch* 64, 1986, Herb. Christ, not seen at P; fragment, *Münch* s.n. US!

This species was first collected in Mexico by Liebmann, who obtained large specimens now in the Folio Herbarium at Copenhagen. It was later introduced into cultivation by Linden and it soon received the name *Cibotium princeps* in the horticultural literature. The early association of the species with the genus *Cibotium* obviously was based on the prominent whitish undersurface of the leaf, especially evident in sterile materials. When plants from the Linden introduction became fertile John Smith placed the species in *Cyathea*.

This is the largest species of the group, with trunks to 15 m. tall and to 40 cm. in diameter. The leaves are up to 5 m. long with massive petioles. In Guatemala it is appropriately known as "Palma de Montaña" while in Mexico it is called "Rabo de Mico" from the furry appearance of the scaly crozier when it has an elongate petiole with the coiled lamina at the apex. The close relation of *Sphaeropteris horrida* and *S. insignis* has been mentioned under the latter species, as well as some frequently distinguishing characters not mentioned in the key. The indusium of *Sphaeropteris horrida* is often opaque but it rarely varies to translucent (*Brenkle* 47-103).

Sphaeropteris horrida grows in the moist mountainous regions of southern Mexico, Guatemala and Honduras at ca. 600-1800 m. Additional specimens seen:

Mexico. VERACRUZ: near Córdoba, *Spence* 125 (GH); Fortín, *Copeland* G (US); region de Orizaba *Bourgeau* 2794 (P, in part). OAXACA: Lavani to Tepinapa, *Reko* 4059 (US), vicinity of Cafetal Concordia (transplanted to hort. from Pluma Hidalgo), *Morton & Makrinius*

2681 (F, US). CHIAPAS: Hacienda Monserrate, (sw. of Cintalapa, near Oaxaca border), *Purpus* 9197 (F, GH, MO, NY). **Guatemala.** Salvin (GH). HUEHUETENANGO: between Ixcan and Finca San Rafael, Sierra de los Cuchumatanes, *Steyermark* 49402 (F, GH, US); Cerro Negro, 2 miles e. of Las Palmas, Sierra de los Cuchumatanes, *Steyermark* 51704 (F, GH, US). QUEZALTENANGO: Finca Chicabal, above Colomba, *Standley* 68044 (F); near Calahuaché, *Standley* 67096 (F); south facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, *Steyermark* 33178 (F), 33192, 33297, 33330, 33432 (F, US). SUCHITEPÉQUEZ: Volcán Santa Clara, 2 miles w. of Finca El Naranjo, *Steyermark* 46822 (F, GH, US); Volcán Santa Clara, above Chicacao, *Steyermark* 46771 (F, GH, US); Finca Naranjo, Chicacao, *Brenkle* 47-103 (F, NY). ALTA VERAPAZ: Finca Sapacueté, Senahú, *C. L. Wilson* 218 (F); Finca Seamay, Senahú, *Hatch & Wilson* 135 (F); vicinity of Secanqúin, *Cook & Doyle* 40 (US); between Tactic and Tamahú, *Standley* 90732 (US); Río Frio, s. of Santa Cruz, *Standley* 90175 (F, US); Cobán, *Turckheim* II 1545 (F, MO, P), in May, 1886 (J. D. Smith exsicc. 24) (B, GH, NY, P). CHIQUIMULA: Cerro Tixixi (Tishishi), 3-4 miles n. of Jocotán, *Steyermark* 31577 (F). **Honduras**: Atlántida: Lancetilla Valley, near Tela, *Standley* 53974 (F, US). COMAYAGUA: Barranco de Trincheras, 16 km. from Siguatepeque, *Molina* 7914 (US), Trincheras, n. of Siguatepeque, *Steeves & Ray* 484 (GH).

3. **Sphaeropteris Brunei** (Christ) Tryon, Contrib. Gray Herb. 200: 20. 1970. Map B. Figs. 9-14.

Cyathea Brunei Christ, Bull. Herb. Boiss. II, 4: 947. 1904. Holotype: Costa Rica, *Brune & Wercklé*, Herb. Christ, P! (a sterile pinna, the fertile material described by Christ, not seen). *Wercklé* in 1903, A!, NY! and *Wercklé* in 1901-1905, NY! ex Christ are doubtless authentic.

Cyathea caesia Christ, Bull. Herb. Boiss. II, 7: 272. 1907. Lectotype: La Palma, Costa Rica, 1500 m. 24 Nov. 1905, *Wercklé* (Herb. Instit. phys.-geog. nat. costarric. 17008), Herb. Christ, not seen at P. Isotype: (differing in date: 24, IX, 1905) P!

Sphaeropteris Brunei and the next species *S. Cuatrecasasii* are notable for the long-persistent large scales which may wholly conceal the petiole in mature leaves. This is somewhat variable in *S. Brunei*, however, and sometimes the scales are persistent only toward the base of the petiole. *Sphaeropteris Brunei* is variable in other characters, for

example, the petiole scales are usually whitish but sometimes they are brown, and sometimes are sparingly rather than freely dentate, the sterile segments are sometimes nearly devoid of indument, and the details of the indument on the lower surface of the segments are not always constant. The extent of this variation in the Costa Rica and Panama materials makes the taxonomic disposition of the collections from the Sierra Nevada de Santa Marta somewhat uncertain. The geographic isolation might imply that the Santa Marta material represents a separate taxon but it differs from most specimens from Central America in only two characters. These are the costule scales on the abaxial surface which are mostly light-colored and concolorous or nearly so and have light colored cilia, rather than being darker at the base and with dark colored cilia. However, two collections from Costa Rica, *Scamman* 7583 and *Molina et al.* 18085 have some scales very like those of the Santa Marta collections.

Sphaeropteris Brunei grows in the montane forest of Costa Rica and in one region of Panama, also in the Sierra Nevada de Santa Marta, Colombia, at altitudes of 800-2000 m. Additional specimens seen:

Costa Rica: *Wercklé* in 1907 (P); vicinity of Coliblanco, *Maxon* 332 (NY, P). HEREDIA: Cinchona, above the upper Sarapaquí valley, *Scamman* 7582 (GH). AIAJUELA: near Zapote, on road to Villa Quesada, *Scamman* 7583 (GH); Carilblanco, ca. 10 km. ne. of Volcán Poas, *Nisman* 114 (GH); Carrizal toward Cariblanco, *Gastony* 795 (GH). SAN JOSÉ: La Palma, *Maxon* 487 (NY, P); La Palma, *A. & C. Brade* (Rosenst. Fil. Costaric. Exsicc. 30) (A); above La Hondura, *Gastony* 768 (GH); Las Nubes, *Scamman & Holdridge* 7859 (GH); San Isidro El General, *Nisman* 41 (GH), *Molina et al.* 18085 (F). CARTAGO: on road up Turialba Volcano, nw. of Trinidad, *Lent* 559 (GH). **Panama.** CHIRIQUI: valley of the Río Caldera, El Boquete to the Cordillera, *Killip* 5242 (GH); Holcomb's Trail, 10 miles above El Boquete, *Killip* 5242 (US). **Colombia.** MAGDALENA: Sierra Nevada de Santa Marta; Alto de Cielo, Dec. 12, *H. H. Smith* 1122 (GH, NY), above Las Nubes, Feb. 6, *H. H. Smith* 1122 (NY), without precise locality, *H. H. Smith* 1122 (F, MO, NY).

4. **Sphaeropteris Cuatrecasasii** Tryon, spec. nov. Map B. Fig. 15-17.

Species *Cyathea Bruneo* valde affinis, differt squamulis minutis petioli rufis fortiter dissectis substellatis brachiolis paucis, squamis costulae subter basaliter brunneis versus apicem pallidioribus ciliis pallidis. — Caulis erectus 3 m. altus 15-20 cm. crassus, petiolus 1.25 m. longus dense persistenter squamatus squamis cellulis conformibus marginibus ordinatim fusci-denticulatis setulas fuscas ad apicem ferentibus, lamina 2.5 m. longa bipinnato-pinnatifida infra pallida, pinnulae segmentis basalibus plerumque auriculatis abrupte excavatis, costa et costula subter squamis fere planis, indusium globosum. Holotypus: Colombia. Valle del Cauca: Filo de la Cordillera Occidental, sobra Las Brisas, entre El Tabor y Alto de Mira (ca. 20 km. wnw. of Cartago), *Cuatrecasas* 22423, US. Isotypus: F.

Sphaeropteris Cuatrecasasii is especially distinguished by the covering of distinctive reddish squamulae (Fig. 15) of the petiole which are borne beneath the large scales and form a dense layer concealing the petiole surface. Characters of the costule scales are mentioned in the key but considering the variation among these in *Sphaeropteris Brunei* (where they are rarely nearly like those of *S. Cuatrecasasii*) they may well be found to be variable in *S. Cuatrecasasii* as additional materials of it become known. Squamulae similar to those on the petiole are also present on some of the abaxial surfaces of the pinna rachises where they are sparingly persistent on the mature leaf. A further character that is difficult to assess is that in *Sphaeropteris Cuatrecasasii* the surface of the larger petiole scales is quite dull (below their apical portion) due to the irregular surface. In *S. Brunei* the surface of the petiole scales is smooth or only slightly irregular and is shining.

The single collection was obtained at 2200-2300 m. in central Colombia.

5. **Sphaeropteris quindiuensis** (Karst.) Tryon, Contrib. Gray Herb. 200: 20. 1970. Map C. Figs. 18-22.

Cyathea quindiuensis Karst. Linnaea 28: 454. 1857. Holotype: Crescit in tractu montuoso Quindiuensi inter flumina

Magdalena et Cauca, Colombia, *Karsten*. Páramo Quindío, 7000 ft., *Karsten*, det. Karsten Herb. Mett. B! is authentic as may be Colombia, *Karsten*, fragment ex Rosenst. US!

Cyathea crassipes Sodiro, Rec. crypt. vasc. Quito 10. 1883. Lectotype: San Florencia, Ecuador, 5/1882, *Sodiro*. Isotypes: A! MO! P! US! (An apparently different collection, with the same data, is at NY). Paratypes: Nanegal, Ecuador, *Sodiro*; Santo Domingo, Ecuador, *Sodiro*.

Cyathea Bonapartii Rosenst. Fedde Repert. 7: 289. 1909. Holotype: Monte Canelos inter Río Verde et Mapoto, Ecuador, Oct. 1857, *Spruce*, Herb. Bonaparte 10049, P!, fragment ex Bonap. US!.

Cyathea yungensis C. Chr. Ark. f. Bot. 20A(7) : 10. 1926. Holotype: El Chaco, Prov. Sur Yungas, Dept. La Paz, Bolivia, ca. 2000 m., *E. Asplund* 1273, probably UPS. Isotype: Herb. Birger, S-PA! (det. C. Chr. with an unpublished name).

The bullate scales on the abaxial surface of the costules (Fig. 22a, 22b) serve to distinguish *Sphaeropteris quindiuensis*. It is a variable species in a number of characters, including the abundance of the bullate scales which may be few to many on a costule. The color of the petiole scales varies from usually whitish to lustrous brown and their margin varies from regularly to very sparingly dentate. The ultimate segments are usually approximate and adnate (Fig. 20) but (especially in Peru) they vary to rather widely spaced and subsessile toward the base of the pinnules. The scales on the costa, beneath, are variously bicolorous to multicolorous or rarely brown and concolorous (*Little* 8038) and the scales on the lower surface of the costules may be darker basally or darker apically, or concolorous, and they may or may not have a long trichomoid tip. A few simple or branched trichomes may be present on the under surface of the segments or they may be rather abundant (*Sparre* 16337).

Sphaeropteris quindiuensis grows in the Andes of Colombia, Ecuador, Peru and Bolivia, at ca. 1400-2700 m. Additional specimens seen:

Colombia. CALDAS: Old Quindío Trail, Laguneta to Magana, *Killip & Hazen* 9473 (GH); Quindío, *Triana* (P), fragment of *Triana* 185 (B). TOLIMA: El Aden to La Palmilla, *Killip & Hazen* 9622 (GH, NY, US). HUILA: Hacienda Balsillitas, Meta to El Cedral, *Little* 8038 (GH, US). PUTUMAYO: Sibundoy, *Schultes & Villarreal* 7711 (GH). **Ecuador.** PICHINCHA: Valle Lloa, *Mille* (P, US); Vulcán Corazón, *Sodiro* in May 1902 (A, NY, P); Monte Pichincha, *Sodiro* in Sept. 1900 (NY); Vulcán Atacatzo, *Sodiro* in July, 1907 (P); Chiriboga, *Sparre* 16990, 16995, 17390 (GH, S); Chillagallo to Chiriboga, *Sparre* 16871 (GH, S); Nono to Tandayápi, along Río Alambí, *Sparre* 19360 (GH, S). TUNGURAHUA: near Baños, *Sydow* 511, 702 (US); Baños, *Heinrichs* 254 (F); Vulcán Tungurahua, *Sodiro* in Dec. 1904 (F, US). ZAMORA-CHINCHIPE (Santiago-Zamora): Loja to Zamora, *Sparre* 16337 (GH, S). **Peru.** HUÁNUCO: Tingo María to Chinchao, Río Chinchao, *Soejarto* 1427, 1430 (GH); Playapampa, *Macbride* 4856 (F). PASCO (formerly in Junín): Oxapampa, *Soukup* 2336 (F, GH, USM).

6. **Sphaeropteris Gardneri** (Hook.) Tryon, Contrib. Gray Herb. 200: 20. 1970. Map C. Figs. 23-24.

Cyathea Gardneri Hook. Sp. Fil. 1: 21, *t.* 10A (cited as 10B). 1846. Lectotype: Arrial das Merces, Brazil, *Gardner* 5328 K!, fragment NY! Isotypes: F! (fragment ex P), P! US! Paratype: Morro Velho, Brazil, *Gardner* 5333, K!, fragment NY!

Cyathea incurvata Kze. Linnaea 22: 579. 1849. Holotype: Caldas, Minas Geraes, Brazil, *Regnell* I 477, fragment P! (Herb. Luerssen ex Herb. Lips. Kze.). Isotypes: B! P! US!

Cyathea mamillata Fée, Crypt. vasc. Brésil 1: 176, *t.* 63, *f.* 2. 1869. Holotype: Serra Carassa, Brazil, *Galeotti* 247. Isotype: P! (*s.n.* in Herb. Glaziou).

Cyathea Taunaysiana Fée, Crypt. vasc. Brésil 1: 178, *t.* 64, *f.* 2. 1869. Holotype: Tijuca, Brazil, *Glaziou* 1701 P! (Herb. Cosson), fragment ex Fee, NY! Isotypes: P! US!

Cyathea attenuata Fée, Crypt. vasc. Brésil 1: 178, *t.* 66, *f.* 1. 1869. Holotype: Minas Geraes, Brazil, *Weddell* 1062. Isotype: P!

Sphaeropteris Gardneri is often a small species, with leaves only about 1 m. long. The abundant simple or branched trichomes on the costules beneath (Fig. 24), are

especially characteristic of the species although they vary somewhat in their density. Scales are usually absent from the abaxial surface of the segments but rarely a few flattish ones may be present.

Glaziou 1701 is considered to be the holotype of Fée's *Cyathea Taunaysiana* on the basis of evidence that Cosson obtained portions of Fée's own herbarium. There is a complete set of the Glaziou collections of tree ferns, cited by Fée in his Crypt. vasc. Brésil., present in the Cosson Herbarium at Paris and some collections that have special parts of the plant have an obvious identity with the illustration published by Fée. Some of the sheets also have original pencil drawings attached that match the illustrations. I believe that Cosson acquired some parts of Fée's Herbarium, certainly the materials of the Brazilian Cyatheaceae, and probably all of those relating to his Brazilian work.

The several collections seen provide no information on the habitat or altitude but the localities are all from the mountainous regions of São Paulo, Rio de Janeiro and Minas Geraes. Additional specimens seen:

Brazil. *Burchell* 4703 (B, P). MINAS GERAES: *Widgren* in 1844 (GH, US), in 1845 (US); entre Sitio y Barbacena, *Glaziou* 11710 (B, NY, P); Saramento, *Macedo* 2883, 2885 (MO); Caldas, *Mosén* 2033 (B, P), 4588 (P); Barbacena, *Pohl* (P). RIO DE JANEIRO: Petropolis, *Spannagel* 434 (NY); Nova Friburgo, *Glaziou* 2282 (P); *Glaziou* 7329 (B, NY, P); *Glaziou* 981 in 1872 (GH, P) (not *Glaziou* 981 cited by Fée as *Alsophila ceropteris* Fée). SÂO PAULO: Santa Anna, *Brade* 5378 (NY); Ozaco, *Luederwaldt* 643 (NY), 1166 (B, NY).

Acknowledgements

This study was supported by National Science Foundation Grant GB 4184. I am indebted to Marjorie Markel and Lydia Wunsch for the preparation of the illustrations. The officers of the following herbaria have been generous in making materials available for my study: B, BM, C, F, K, MO, NY, P, S, S-PA and US.

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A SECOND RECORD FOR THE GIANT CHICKWEED, MYOSOTODON AQUATICUM, IN NEW HAMPSHIRE: In a moist meadow-pasture along the Connecticut River, one mile south of Monroe, northern Grafton Co., New Hampshire, I found on August 29, 1970 a large number of plants of the giant chickweed, *Myosotodon aquaticum* (L.) Moench. The plant reminded me strongly of *Stellaria pubera*, but I noticed the 5 styles. The only other record for New Hampshire is at Bristol, in extreme southeastern Grafton Co.; however, the plant has been found along the Connecticut River at Bradford, Vermont.

I suspect that the plant occurs in grassy meadows all along the Connecticut River. It is true, however, that forests, rocky banks, and towns come right down to the river at many places. Specimens are being sent to the herbaria of New England Botanical Club, University of New Hampshire, and the Pringle Herbarium, University of Vermont.

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A POPULATION STUDY OF TULOSTOMA BRUMALE

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The subject of this paper, *Tulostoma brumale* Persoon, is the type species of the genus, which belongs to the class Gasteromycetes. The reason for the study is the existing confusion concerning the definition of species within this genus. The authors collected thirty-five plants (Tiffney and Tiffney, 1965) in 1963. When we attempted to identify our collection we found it possible to relate individual specimens to several species within the genus. After examining specimens in the herbarium of the New York Botanical Garden and in the Farlow Herbarium we concluded that considerable synonomy exists within the genus. This condition has existed for some time. G. H. Cunningham in 1925 stated that ". . . confusion exists in the delimitation of species, and by certain workers the genus is considered to be the most difficult of any included in the Gasteromycetes".

The problem became even more obvious in 1964 and again in 1965 when more specimens were collected from the same location as the 1963 material. We now had 88 specimens taken over three years, all from the same spot, but many differing in appearance sufficiently to raise a question as to their identity. Some were small in a dry year, others larger in a wet year, and all possessed sufficient variations to warrant the belief that certain characteristics were of little value in determining species in the genus. Had we used keys published by several authors or followed identifications suggested on the specimens we examined in various herbaria as our guide we could have reported the collection of several species of the genus *Tulostoma*, all for the first time in the New England area and all from one small location. Such an occurrence appeared to be most unlikely.

We postulated that our collections had to be considered as all belonging to one species but representative of the variation mentioned by White (1901), Lloyd (1906), Cunningham (1925 and 1942) and Long (1947). At the time

we first found these plants in 1963 they were limited to a small area of sand dune about 25 feet wide and 70 feet long. They spread to successively wider areas in 1964 and 1965, and by 1968 were found over an area of some five acres. It is probable that the introduction of the original spores occurred only slightly prior to our initial discovery in 1963. This introduction appears to have been an isolated occurrence, perhaps accomplished by a "well-traveled" horse.[1] Long and Ahmad (1947) note that *Tulostoma* spreads rapidly from spores in India. Coker and Couch (1928) note the perennial nature of plants of this genus and report one species as persistent on the same site for 19 years. Perennial and spreading rhizomorphs may also give rise to new plants on the same site. The extensive diversity observed in size and other characteristics in our material probably is due to environmental influence and natural capacity for variation within the population and not to genetic exchange with other *Tulostoma* species. The nearest reported station to ours is Ithaca, New York, by White (1901). Both authors and their students have collected extensively along much of the New England coastline, and although we have been looking for *Tulostoma* ever since the first collection, we have yet to discover a second station; therefore we feel that the Cape Ann material is isolated from other *Tulostoma* populations.

The 88 specimens forming the basis for this study were collected on a public bathing and recreation area at Good Harbor Beach in Gloucester, Essex County, Massachusetts. The plants (Fig. 1) grow in sand dunes near the storm beach, in a band some 150 to 300 feet back from the normal high tide line. The area is only slightly protected from the

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[1]Lloyd (1906) notes that *Tulostoma campestre* is common where "Horses had evidently been in the habit of resting there in the shade". Good Harbor Beach, where our collections were made, is an area used for exercising horses by Cape Ann residents. The spores may have been introduced to the area in the feces of one of these herbivores.

open ocean by the low, 8 to 10 foot fore-dune. The pH in this area ranges from 7.0 to 7.8, undoubtedly resulting from salt spray from ocean storms, as New England soils with but few exceptions are acid. The tolerance of certain members of the genus to basic soils and to salts is well documented by Long and Ahmad (1947) working in India, when they note the presence of "many *Tylostoma* collections" coming from "kallars" or pans whose surfaces may become covered with white incrustations of salt in dry weather. This tendency was mentioned earlier by Long (1944).

The beach faces southeast to east, the direction of many of the severe storm winds of this area. The soil is composed of wind blown sands, derived from the beach area, bound loosely in place by *Ammophila breviligulata* Fernald, a coarse perennial beach-grass. What organic material there is in these sands appears to be derived from the decay of the rhizomes and leaf blades of this grass. Indeed the rhizomorphs of the collected *Tulostoma* frequently penetrated the decayed grass materials. The entire beach is about 10 to 15 acres in extent and rests on a typical estuarine salt marsh of 30 to 40 acres, bounded by a semicircle of low granitic hills, with the exception of the edge facing the sea. To the best of our knowledge the population of *Tulostoma brumale* reported here has not yet migrated out of this relatively limited area.

Priority in the Gasteromycetes begins with the work of C. H. Persoon (Synopsis methodica fungorum, 1801). He assigned the name *Tulostoma brumale* to a form previously recognized by Linnaeus (Species plantarum, 1753) as *Lycoperdon pedunculatum*, an organism apparently of general north European distribution.[2] Later C. Sprengel (Systema vegetabilium, ed. 16, 4 (1) 1827) revised the spelling

[2]Although Lloyd (1906) feels it cannot be found in England, this form is apparently distributed in the Low Countries around the North Sea as well as in Italy, Austria, Switzerland and Hungary. Cunningham (1942) reports it from Australia and New Zealand, and Long and Ahmad (1947) from India, thus it appears to have a cosmopolitan distribution.

Fig. 1. *Tulostoma brumale* Persoon growing in sand dunes 150 to 300 feet back from the storm beach, in the spray zone. The sand is stabilized to some extent by *Ammophila breviligulata* Fernald, which appears to be the source of organic material for the fungus.

of the genus to *Tylostoma* thinking apparently the original to be an orthographic error. As stated in an earlier paper (Tiffney and Tiffney, 1965) we are retaining Persoon's spelling.

We now believe the description of the species must be enlarged to include the considerable variation in size and form possible under varying climatic conditions. It is hoped that this study will aid in reducing the confusion concerning the number of species within the genus. While we do not believe that a study involving even the simple type of statistical functions performed here is required of an investigator each time he collects a species of this genus, we do feel statistical analysis necessary in the current work to describe permissible bounds of variation for the species *Tulostoma brumale* and to establish its position within the genus.

The high degree of variation that exists within species of *Tulostoma* suggests the futility of erecting species based on the examination of a few plants collected over a single growing season. Cunningham (1925) stated this problem, "The difficulty is to decide which are fixed characters in such a variable genus; about half of the species which have been described to date cannot be separated on any recognizable character". Lloyd (1906) notes that species should not be described from single collections, and Cunningham (1942) further states, "About 85 species have been described, of which not more than 30 are valid".

Long (1944) proposed a list of characters he thought necessary to differentiate the species within this genus. As the list appears quite inclusive, we have used it as our standard. We have used two approaches in analyzing this list. The first consists of characters that can be measured to the nearest millimeter or micron, and these have been treated statistically, while the second group of criteria is subjective in nature and requires a percent-presence approach to render them amenable to numerical analysis. The characters measured and subjected to statistical analysis were height of the entire plant, stipe height, sporocarp

height and width, and spore diameter. Gross characters were measured to the nearest millimeter, spore diameter to the nearest micron. Spores from each plant were placed on a microscope slide and heated in 5% potassium hydroxide to re-expand them to their original and typical size. This procedure is recommended by Cunningham (1925) and was found to give excellent results when dried material was to be compared with fresh. The average spore diameter is based on a sample of 100 spores from each plant.

The plants were arranged in three groups corresponding to the years of collection: 1963, 1964 and 1965. As these collections constitute a geographically and therefore genetically isolated population of *Tulostoma*, variation may be ascribed to individual genetic diversity inherent within the organism plus variation caused by climatic changes acting within individual growing seasons. Long and Ahmad (1947) have suggested that availability of moisture to the *Tulostoma* plant at the time of stipe elongation and sporocarp expansion has a profound effect on the proportions of the mature plants. Our Cape Ann material apparently expands and appears above ground in late October. The United States Weather Bureau records for nearby Rockport, Massachusetts, show October rainfall for our 1963 collection to be 6.95 inches, for the 1964 collection 5.31 inches and for the 1965 collection only 1.97 inches. The 1965 group had very low moisture available to it during the critical expansion period, while both the 1963 and the 1964 groups had a normal and adequate rainfall.

Table 1 gives comparative values for the range, mean, and standard deviation for each of the three groups and each of the measurable characters within these groups. The table shows that in the character of height of the entire plant the 1965 group is the smallest, while the 1963 group has the greatest range and the 1964 material averages largest. Adequate and similar quantities of rainfall resulted in the larger size of the 1963 and 1964 collections while low precipitation in 1965 is reflected in the small stature of plants for that year. Stipe height figures follow

the same pattern; the 1965 material averages smallest, the 1963 plants have the greatest range, and the 1964 plants average largest. However, the character of sporocarp height in the three groups shows less variation as a result of differing rainfall quantities than do the above characters. The 1964 group is unaccountably larger than either the 1963 or the 1965 collections. The same statement holds for sporocarp width. In contrast to the extensive differences noted for gross measurements, spore diameter appears to be a rather consistent figure for the three groups. The greatest range occurs in the 1963 group, 3.88μ to 5.72μ. The mean is slightly higher in 1964 and the overall size variation less in 1965. In general spore size is the most consistent measurable character found in our material.

Table 1

	Group 1, 1963	*Group 2, 1964*	*Group 3, 1965*
		Height Entire Plant	
Mean	49.00 mm	54.24 mm	39.25 mm
Range	21-99	25-72	25-83
Std. Dev.	16.53	10.70	12.92
		Stipe Height	
Mean	43.94 mm	46.21 mm	33.80 mm
Range	17-93	21-65	20-74
Std. Dev.	15.30	10.70	11.83
		Sporocarp Height	
Mean	5.09 mm	8.03 mm	5.45 mm
Range	1-11	4-12	3-12
Std. Dev.	2.37	1.99	1.94
		Sporocarp Width	
Mean	8.34 mm	11.30 mm	7.50 mm
Range	4-14	5-17	5-13
Std. Dev.	3.07	2.59	2.13
		Average Spore Diameter	
Mean	4.81 μ	5.00 μ	4.34 μ
Range	3.88-5.72	4.15-5.66	3.96-5.15
Std. Dev.	0.4459	0.3470	0.3012

Table 1. Comparison of the 35 plants collected in 1963 having 6.95 inches of rainfall during their period of elongation and development with the 33 plants collected in 1964 having 5.31 inches of rainfall and with the 20 plants collected in 1965 having only 1.97 inches of rainfall.

There is a relationship between rainfall during the growing season and size of plants. More rainfall during this critical period gives larger plants, less yields smaller plants. We now wished to find if the ratios of the sizes of measurable parts of these larger and smaller plants were consistent. A coefficient of correlation test was performed on each measurable part of all plants in the three groups. For example, a positive coefficient of correlation result of .60 indicates that the two items measured increase together 60% of the time, while 40% of the time one variable increases and the other either stays the same or decreases. Our results showed that in general a *Tulostoma brumale* plant increases proportionately in size. This relationship holds true between 22% and 99% of the time and averages 63% for our material, based on 30 tests comparing all measurable parts of the plants with all other measurable parts. The least correlation, 41%, was achieved when comparing sporocarp height with stipe height. This is reasonable as the sporocarp collapses with the liberation of the spores. Spore diameter correlated rather poorly with stipe height, 45%, indicating a fairly tenuous relationship between height of the plant and size of spores. Spore diameter correlated fairly well with the height and width of the sporocarp, 62%, indicating that in general larger sporocarps produce larger spores. Macroscopic plant parts (height of the entire plant, stipe height, sporocarp height and width) correlated well, at 68%. The plant, at least internally, is fairly consistent with its parts increasing proportionately 63% of the time.

Coefficient of correlation results indicate that an individual plant is at least reasonably consistent in the relationships of its measurable parts. However the plants of the three yearly collections, taken as groups, appear to differ widely when viewed in the light of range, mean and standard deviation data presented in Table 1. We have suggested that this group variation may be due to differing amounts of rainfall during the various growing seasons.

We wished to test the significance of these yearly group

variations statistically. We employed the combination of the "F" test with the Duncan Multiple Range test. The "F" test determines within certain probability ranges if the means of sample groups (in our case the three collections) are sufficiently similar to assume that the sample groups were originally drawn from a single larger aggregate, or if the sample groups are sufficiently dissimilar to assume that they are separate entities. If the first case is true, then the yearly collections are part of a single though variable population, and species in *Tulostoma* may be defined by reasonably narrow ranges of measurable characteristics. If the second case is true, then either the three yearly collections represent three separate species or environmental factors cause much greater variation in measurable portions of the plant than has been previously thought. In this case only the broadest approach to species determination by measurable characters should be used. As before the "F" test and Duncan Multiple Range test were aplied to all measurable parts of the plants, comparisons being made among height of the entire plant, stipe height, sporocarp height and width, and average spore diameter.

The "F" test results confirmed that the second case was true and that the three groups were significantly different. Significance was confirmed among the groups for all measurable characteristics including spores at the 0.005% confidence level.[3]

The "F" test results state that significant differences exist somewhere among the three groups but do not state specifically whether these differences exist between the 1963 and 1964 groups, or between the 1963 and 1965 groups, or between the 1964 and 1965 groups, or all three. With "F" test results available the Duncan Multiple Range Test does just this. The Duncan test shows that significant dif-

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[3]The 0.005% confidence level indicates that the conclusion suggested by "F" test results will be correct in 99.5% of all cases. (Pearce, 1965)

ferences at the 0.05% level[4] exist for all characters between all three groups with one exception in the 15 tests performed. The exception is that no significance was seen for spore diameter between the 1963 and 1964 collections.

The Duncan test clearly locates a fact indicated by the "F" test, that with the exception of spore diameter (one out of fifteen tests performed), the 1963, 1964 and 1965 collections are quite different from each other. Had we not possessed complete collection data for these collections, if for example we had been working with scattered herbarium specimens, we could statistically justify erecting three (or at least two) further species in this already over-crowded genus.

The conclusion that we have new species is unacceptable in the light of our complete data. As we stated earlier, the limited area to which these plants are confined, their slow spread from an initial site during the years 1963 to 1968 and our inability to locate other colonies in New England all logically require that our three collections represent a single species. This apparent conflict between statistical and biological evidence does not indicate that either is wrong. Rather than assessing inherent characteristics of plants, the statistical procedures are indicating that variation in some environmental factor, perhaps rainfall, is expressed as variation in each yearly group of *Tulostoma* plants.

The form, size and distribution of *Tulostoma* plants may be potentially affected by other physical and biotic factors. Variation of pH in turn influenced by salt spray blown in high winds may determine the areas of the beach available for colonization as well as the dimensions of the mature plants. Perhaps higher rainfall by its leaching effect would reduce the salt content of the sand. The 1965 plants were subjected not only to a lower rainfall but also to a slightly higher soil-salt content during their growing season. Long

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[4]The 0.05% level indicates that conclusions suggested by the Duncan test will be correct in 95% of all cases. (Duncan, 1955)

and Ahmad (1947) suggest that matted grasses of several species restrict or distort emerging *Tulostoma* plants in India and may preclude growth of plants in areas of thick grass cover. Our material was taken from a well-stabilized area of sand dunes with a characteristic open cover of *Ammophila breviligulata* Fernald. *Tulostoma* does not occur on Good Harbor Beach in areas of dense grass cover. Many plants were collected with their rhizomorphs entangled with or penetrating decaying *Ammophila* rhizomes. This was presumed to be the normal supply of organic material for the fungi. Long and Ahmad (1947) further note that excessively hard soils lead to restricted or atypical development, while excessively soft substrates allow the plants to be dislodged by rain and wind. Our material grew in an intermediate position somewhat back from the fore-dune between the actively moving beach and the well established area. Most of our plants are well developed or at least undistorted. Some few distorted plants were collected from marginal habitats in areas of loose sand or extensive grass cover. In general there is little doubt that environmental factors with rainfall prime among them are responsible for extensive variations in populations of *Tulostoma.*

It is now possible to comment on the reliability of measurable characteristics in regard to separating species in the genus *Tulostoma.* Spore diameter is the most consistent character among those examined. Dramatic differences in spore diameter could, if found, prove useful in determining species; however variation even in this measurement in our material is sufficient to warrant adopting wider boundaries. Gross measurements are highly variable; of these, height characters including height of the entire plant and stipe height exclusive of sporocarp are the most consistent, but dimensions of the sporocarp itself are so variable as to be nearly useless. All these dimensions have been treated in the literature as having diagnostic value (Long, 1944). Gross measurements in general should be used with only the widest boundaries in species determination.

When we compare our measurable characteristics with

Table 2
Published Measurements for *Tulostoma brumale*

	Stipe Height	Sporocarp Height	Sporocarp Width	Spore Diameter
White, 1901	10-50 mm	10-15 mm	10-20 mm	3-5 μ
Lloyd, 1906	—	—	—	5
Coker & Couch, 1928	10-20	—	6-10	3.8-4.5 × 4.0-5.5
Cunningham, 1942	20-40	—	12 max.	4-6
Smith, 1951	10-50	10-15	10-12	3-5
Maximum Dimensions	10-50	10-15	6-20	3-6
Tiffney & Tiffney	17-93	1-12	4-17	3.88-5.72

Table 2. Measurements given by various authors for the described characters of *Tulostoma brumale* plants compared with our results.

those set by other authors (see Table 2) for *Tulostoma brumale* we find that our figures show a wider range for the species but the means appear to be in general agreement with those in the literature. However when we turn to a consideration of those qualities which compose the bulk of most species descriptions in taxonomic publications, the subjective delineation of the form of the plant, color of various parts and vestiture or surface appearance of such structures as the peridium, spores or stipe, we discover that our descriptions and those of the literature are in disagreement. Part of the problem is created by the conventions used in writing such descriptions. While phrases such as "globose to subglobose" are vague but with experience understandable, statements such as "occasionally wanting" and "present or absent" serve no informative function at all. Comparative data of a qualitative nature are necessary for an adequate description.

We have attempted such a qualitative approach below. Characters are listed by their percentage of presence in the specimens examined, using Long's (1944) suggested list of diagnostic characters for the genus. This approach permits a type of quantitative analysis and requires an actual count of all specimens, where previous descriptions have utilized only a "feeling" for the characters, often from a

relatively small number of specimens. Moreover our method requires the investigator to note variations occurring over several growing seasons.

Group 1, 1963.

STIPE: mycelial strands mostly lacking (85%); texture variable, lightly ribbed in about half the specimens (43%) and the rest lightly to heavily scaled (57%); rarely with sand-flocci (6%); color mostly light brown (77%), occasionally gray-white (14%), rarely medium brown (9%).

SPOROCARP: shape mostly subglobose (89%); exoperidium texture with sand-flocci aggregates (100%); endoperidium color mostly gray-white (77%), occasionally light yellow or brown (17%), rarely pure white (3%), or dark brown (3%).

MOUTH: mostly tubular (74%), rarely lacerate (8%); occasionally with a small raised mat (20%).

BASE: highly variable, frequently bulbous (69%), a few volvulate (13%) and an equal number with indistinct bases; mostly with both fibrils and rhizomorphs (89%).

Group 2, 1964.

STIPE: mycelial strands mostly present (94%); lightly ribbed in some specimens (18%), mostly lightly scaled (76%), never heavily scaled; about half with sand-flocci (63%); color mostly light brown (79%), occasionally gray-white (18%), rarely medium brown.

SPOROCARP: shape mostly subglobose (81%); exoperidium texture with sand-flocci aggregates (88%); endoperidium color mostly gray-white (85%), occasionally light yellow or brown (15%).

MOUTH: frequently lacerate (45%), occasionally tubular (15%); mostly with a large or small raised mat (82%).

BASE: highly variable, mostly bulbous (69%), a very few volvulate (7%), or with indistinct bases (24%); mostly with both fibrils and rhizomorphs (89%).

Group 3, 1965.

STIPE: mycelial strands mostly lacking (90%); mostly

lightly ribbed (80%), occasionally lightly scaled (15%), never heavily scaled; mostly with sand-flocci (80%); color almost equally divided between light brown (55%) and gray-white (40%), with a few dark brown (5%).

SPOROCARP: shape mostly subglobose (70%); exoperidium texture with sand-flocci aggregates (60%); endoperidium color mostly gray-white (85%), occasionally pure white (20%), rarely light yellow or brown (10%).

MOUTH: mostly tubular (85%), occasionally lacerate (10%); rarely with a large or small raised mat (10%).

BASE: highly variable, about half bulbous (55%), almost half volvulate 45%); three-fourths with fibrils (75%), one-fourth with rhizomorphs (25%).

Stipe characteristics within the three groups were so highly variable that they could not be used to distinguish the groups from one another. Only in color was there consistency, and stipe color appears to be a factor of soil staining and subsequent bleaching by sun or leaching by rain. Since all plants grow in a restricted area, the color of their stipes should be similar. Sporocarp shape, presence of sand-flocci on the exoperidium and color of the endoperidium were quite generally similar. Mouth shape and vestiture, considered so important for species diagnosis by Coker and Couch (1928), Cunningham (1942), Long (1944), Long and Ahmad (1947) and others, proved to be a quite variable and confusing characteristic for our plants. Indeed, it was at this point that we were forced to turn to herbaria to determine our species. It should be noted that specimens in the herbaria showed more variation in mouth structure than the keys and descriptions in the literature would lead one to expect. Spore size and vestiture may be of some value but we feel that more study of herbarium material is indicated before a final verdict is rendered.

In the hope of making the systematics of this genus less confusing, we offer the following revised species description for *Tulostoma brumale* Persoon 1801 (Synopsis methodica

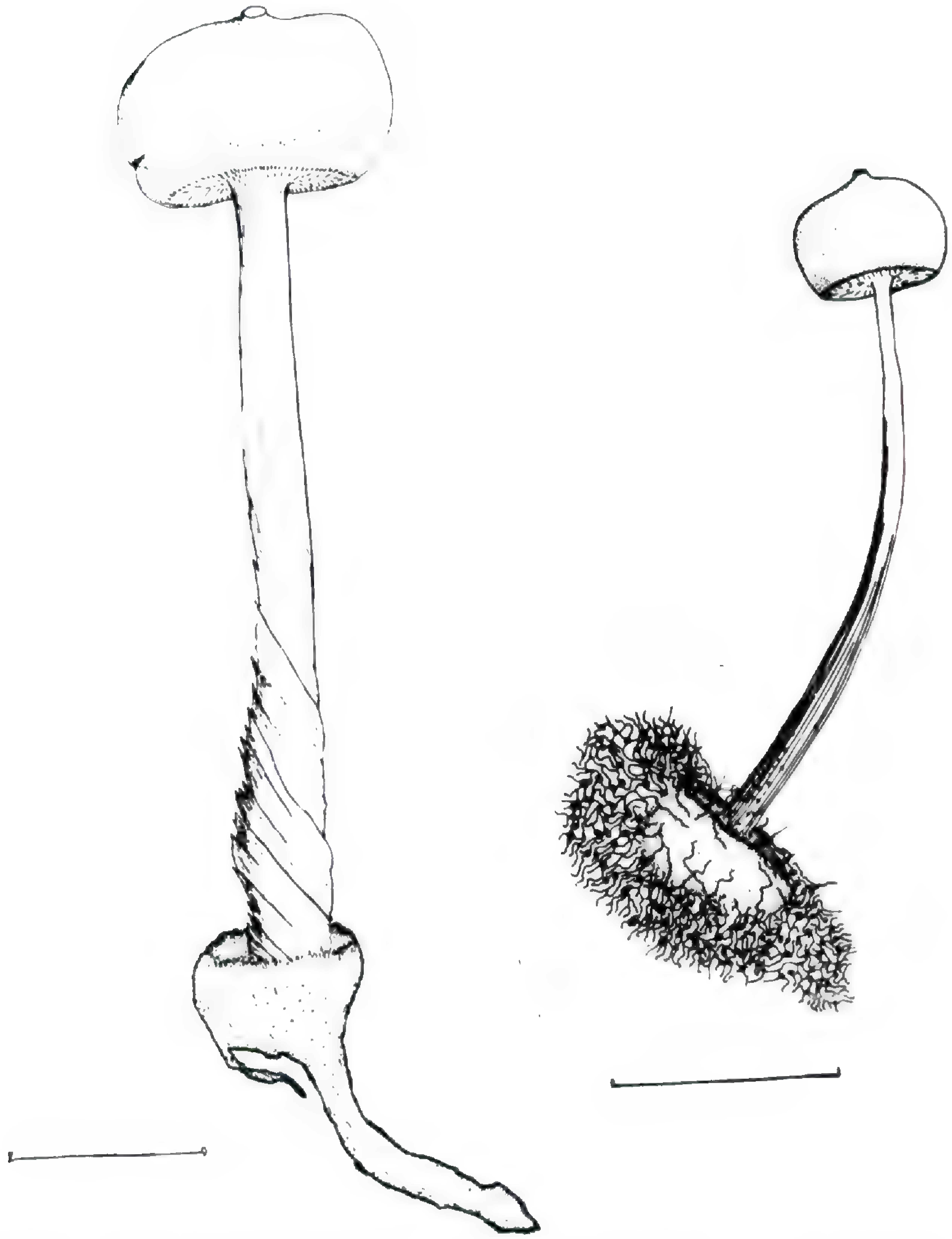

Fig. 2. *Tulostoma brumale*, two plants with bulbous bases, tubular mouths and subglobose sporocarps. The larger plant has an almost smooth stipe lightly scaled at base, the base with a rhizomorph; the smaller plant has a ribbed stipe with the bulb at the base covered with fibrils. The scale lines equal 1 cm. lengths.

fungorum p. 139). We hope it will prove useful in the necessary future taxonomic revision of this group; Figs. 2 and 3 illustrate several features of the species.

The peridium of this organism originates below ground level (hypogeously) at a depth of about 5 to 10 cm. By elongation of a basal stalk it appears above ground (epigeous) in the New England area in mid-October. The early development of spores is in doubt but according to Schroeter (1876) the spores are borne laterally on the basidia. The peridium is composed of two membranes, an outer exoperidium and an inner endoperidium surrounding the spores; numerous unbranched thick-walled sinuous hyphae, the capillitium threads, grow throughout the spore cavity. According to our observations the peridium first appears as a small swelling on the hypogeous mycelium in late August or by mid-September. The exoperidium surface is composed of loosely intertwined slender hyphae which trap the surrounding substrate into the structure, hence the exoperidium is initially the same color as the substrate (5 to 10 cm. deep) in which it developed. It may bleach in sun or wash in rains to a lighter color, sometimes to almost white. The process of emergence of the fruiting body aids in grinding the exoperidium away from the apical portion of the peridium, exposing the endoperidium and leaving the exoperidium persistent only from the equator of the fructification to the insertion of the stalk. The retained portion of the exoperidium is quite fibrous and even in old specimens sand and earth particles of the substrate may be present, coloring this portion of the specimen. Also the exposed exoperidium takes on the soil color through which it has been pushed by the elongation of the stalk. The endoperidium is a tougher, more compact material and lighter in color than the exoperidium. It is a persistent, firm papery structure, smooth to slightly pubescent, and may bleach almost to white in old specimens. Dehiscence is effected by means of a mouth or pore at the apex of the endoperidium. The mouth is usually raised, tubular or umbonate, and may have a smooth or fibrillose area around the opening. In some

Fig. 3. *Tulostoma brumale* with a rather small bulbous base with both rhizomorphs and fibrils, with a ribbed stipe scaled toward the base. The sporocarp is subglobose with just a hint of a tubular mouth but with a tendency to be lacerate.

old weathered specimens and a few new forms an irregular tear may form the mouth opening, thus the appearance of the mouth is variable. The stem is inserted in a socket at the base of the peridium. It may vary greatly in thickness and length. It is smooth in older specimens, or scaly or striate, and is usually hollow with wefts of mycelia in the central chamber. The stem terminates in a bulb, often with an upturned cup-like structure, or it may produce a mass of coarse mycelia which gradually taper off into the substrate. The spores are hyaline to brownish in color, mostly verrucose to warty in surface vestiture. A sufficient number of spiny to almost smooth spores have been observed to make the authors suggest that there is some variation in this characteristic. The capillitium associated with the spores is abundant in some specimens and less in others. These hyphae are smooth-walled, hyaline structures, swollen at the cross walls. The central lumen of the capillitium cells becomes swollen at the septa and narrows in the mid-region. The dimensions of the plant are: height of the entire plant 2 to 10 cm. (20 to 100 mm.), stipe height 1.5 to 10 cm. (15 to 100 mm.), sporocarp height 0.1 to 1.2 cm. (1 to 12 mm.), sporocarp width 0.4 to 1.7 cm. (4 to 17 mm.), spore diameter 3 to 8μ.

Much of the confusion surrounding *Tulostoma* has arisen because investigators described new species from single plants or from only a few specimens. We suggest that some kind of population study, perhaps similar to the one we have performed here, precede the erection of further species in this genus. We feel that we have demonstrated that the type specimen, although useful as a datum point for the name of a given organism, cannot serve as a typical representative of the population or species from which it was drawn. Much synonymy and confusion have arisen in this genus from regarding the type specimen as typical. Although fungi and flowering plants differ greatly, some of the population techniques proved on vascular material may profitably be applied to the higher fungi.

We are indebted to the curators of the Farlow Herbarium

of Harvard University and the Herbarium of the New York Botanical Garden for the opportunity to examine specimens. A large part of the research by the junior author was carried out in association with the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole. Systematics-Ecology Program Contribution No. 222.

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ARTHRAXON HISPIDUS (GRAMINEAE) IN THE UNITED STATES: TAXONOMIC AND FLORISTIC STATUS

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During the fall of 1969, a population of *Arthraxon hispidus* (Thunb.) Makino, attributable to var. *hispidus* according to current treatments of the species, was discovered in an area of Maryland where the typical variety had not been previously recorded. This prompted further inquiry into the status of the species in this country, where both var. *hispidus* and var. *cryptatherus* (Hackel) Honda have been introduced from the native Oriental range of the species (Japan, China, Formosa, New Guinea, Philippines, Indochina, Ceylon, Kashmir and India). Examination of pertinent literature and of numerous specimens attributable to both varieties reveals that the species now has a more intensive distribution within a slightly more extensive range in the United States than at the time of the most complete recent account of it here (Hitchcock, 1950). Such examination also suggests that the species should be treated as a single, quite variable entity rather than maintained with the two varieties heretofore recognized.

Taxonomically, accounts of *Arthraxon hispidus* in this country to the present (Hitchcock, 1935; Blomquist, 1948; Hitchcock, 1950; Fernald, 1950; Gleason, 1952; Weintraub, 1953; Gilman, 1957; Gleason and Cronquist, 1963; Radford et al., 1968) have distinguished the two varieties, though some have accounted floristically for only one of them. Variety *cryptatherus* was first collected in the United States in the 1870's and the varietal name is based on an original quadrinomial proposed in 1889 (*A. ciliaris* Beauv. subsp. *langsdorfii* var. *cryptatherus* Hackel). Prior to that, specimens from this country were attributed to *A. ciliaris* without infraspecific designation or to other entities since placed in synonymy. The typical variety was first collected here in 1933, but was not reported as such in the literature until

1950 (Hitchcock, 1950). *A. hispidus,* and its typical variety, are based on *Phalaris hispida* Thunb., proposed in 1784.

The two varieties of *A. hispidus* are currently distinguished on the following basis: Awns absent, included within the glumes or only slightly exserted, and spikelets "generally smaller" in var. *cryptatherus*; versus, awns long-exsert and spikelets larger in var. *hispidus.* The original descriptions upon which the varieties are based confirm their distinction on these characters alone. Specimens from the United States attributed to both varieties (GH, MARY, US) clearly exhibit general and independent intergradations of these distinguishing characters. Presence of both sets of characters even occurs on the same plant, though infrequently. Examination of numerous specimens from throughout the native Asiatic range of *A. hispidus* (GH, US) indicates that even more intergradation of varietal characters occurs there. This suggests that further establishment of the species in the United States will result in a yet greater range of character overlap than is so far apparent here, approximating that of its native range, where it is very intensively established.

Recent collections from this country indicate that the two varietal conditions occur sympatrically, as is the case throughout the native range. Also, many specimens, from both ranges, with short awns and/or smaller spikelets appear somewhat depauperate. This raises the possibility that environmental factors alone may sometimes account for the occurrence of the set of characters ascribed to var. *cryptatherus.* In at least one case, collections made at the same site but at different times are clearly referable to different varieties (see list of specimens under Montgomery County, Maryland).

In his recent *Flora of Japan,* Ohwi (1965) does not recognize separate varieties of *A. hispidus* and calls attention to the great variability of the species. In line with this modern Asiatic treatment, it is proposed that the same taxonomic view of the species be adopted in this country, for

the following reasons: 1) original distinction of the two character states now attributed to separate varieties of *A. hispidus* occurred at a time when the species was yet imperfectly known but when "splitting" in the genus was rampant; 2) the actual situation obtaining in the species is one of great variability and independent character assortment and intergradation which does not allow a clear enough distinction of separate character complexes to warrant infraspecific division; 3) the two established varieties occur sympatrically and do not, therefore, exhibit any geographical pattern distinct enough to support taxonomic separation; 4) a strong possibility exists that environmental differences over time and space may account for much of the variability observed within the species, including those characters used to distinguish the varieties; 5) occurrence on the same plant of character states attributed to different varieties does not support any biological view of distinct taxonomic entities; and, 6) both characters used for varietal distinction are quantitative rather than qualitative in nature and vary independently of each other in some cases (awn condition is, for all practical purposes, a quantitative character and not one involving presence versus absence of structure — almost all specimens have at least rudimentary awns).

Based upon the above proposal, the nomenclatural status of the species is as follows (only names recently in use and their basionyms are cited):

Arthraxon hispidus (Thunb.) Makino, Bot. Mag. (Tokyo) 26: 214. 1912.

Phalaris hispida Thunb., Flora Japonica 44. 1784.

Arthraxon ciliaris Beauv., Agrost. 111. 1812.

A. ciliaris subsp. *langsdorfii* Hackel var. *cryptatherus* Hackel, Monogr. Agrost. 355. 1889.

A. cryptatherus (Hackel) Koidzumi, Bot. Mag. (Tokyo) 39: 301. 1925.

A. hispidus var. *cryptatherus* (Hackel) Honda, Bot. Mag. (Tokyo) 39: 277. 1925.

The type species of the genus *Arthraxon* is *A. ciliaris* Beauv.

Those so inclined might wish to recognize the two extreme phases of *A. hispidus* at the level of *forma*. However, formal recognition at that level is neither useful nor practicable, except for the separate purposes of micro-evolutionary study, and thus is not here proposed.

Hitchcock (1935), in the first full account of *A. hispidus* in the United States, reported var. *cryptatherus* from Pennsylvania to Florida and from Missouri, Arkansas and Oregon. By 1950, Chase in her revision of that work (Hitchcock, 1950), on the basis of additional collections (some reported in the literature in the interim, see Chase, 1937; Fernald, 1936, 1939 and 1941; Monachino, 1940), reported both varieties as follows: variety *hispidus* from "Maryland (near Washington, D.C.) [not the same location as the new one reported in this paper], Missouri (St. Louis) and Louisiana (Richland Co. [sic])"; var. *cryptatherus* from Pennsylvania to Florida and Tennessee, from Arkansas and from Washington. The treatments by Fernald (1950), Gleason (1952), Gilman (1957; northern Virginia and Maryland only) and Gleason and Cronquist (1963) followed Chase but were less precise and inclusive. Radford et al. (1968) have recently reported new stations in the Carolinas as a result of their intensive study of that area. In addition, evidently on the basis of their current study of the flora of the Southeastern United States, they report the species from Mississippi. Despite the significant contribution of this latter work, the most precise account of *A. hispidus* over its entire range in the United States remains that of Chase.

Based upon specimens examined (GH, MARY, US) and upon the reports by Radford et al. for the Carolinas, *Arthraxon hispidus* (varieties not distinguished) is now known in this country from a wide spectrum of wet to moderately dry habitats, including shallow water, shores of streams and lakes, sand bars, moist bottoms, low woods, ditches, roadsides, fields, gardens and pavement crevices.

The species is distributed here as follows: PENNSYLVANIA: Philadelphia (collections from 1800's only) and locally in Bedford Co. MARYLAND: locally in Baltimore, Montgomery and Prince Georges counties. DISTRICT OF COLUMBIA: locally in the upper Northwest. VIRGINIA: locally in northern counties near Washington, D.C. and southeastern coastal plain counties, and one station in Albemarle Co. NORTH CAROLINA: a few stations in the mountainous western counties, widespread but local in the piedmont (including Rutherford Co., not reported by Radford et al.), and locally in the northeastern and southeastern coastal plain counties. SOUTH CAROLINA: locally in the central and western piedmont and in Chesterfield Co. GEORGIA: locally in the northern counties and in Troup Co. FLORIDA: very locally in the northeastern Panhandle, possibly elsewhere (one collection with location given only as "Florida"). TENNESSEE: locally in Anderson, Campbell and Montgomery counties. ALABAMA: very locally in Talladega Co. and at Auburn. MISSISSIPPI: reported by Radford et al. but no specimens seen. MISSOURI: known only from one station at St. Louis. ARKANSAS: locally in the west-central and northwestern counties. LOUISIANA: locally in parishes close to the Mississippi River above Baton Rouge and one station in Richland Parish. OREGON: known only from one station at Portland.

There is a possibility that the species also occurs in New York. Monachino (1940) reported it from the grounds of the New York Botanical Garden and cited a collection which is presumably on deposit there. Whether the species persists there or occurs elsewhere in the state was not ascertainable from the literature and specimens seen.

Although the above distribution shows only slight change since 1950 in the overall range of the species here, it does show that it has become more firmly established within that range since then (i.e., when compared with the collections upon which Chase's report was based). Most likely, intensive field study, such as that recently done in the Carolinas, will reveal more extensive distributions in some of the other

states within the species range. Perhaps additional locations are already known and can be reported by those actively working with local floras. Certainly the present actual distribution must be greater than what is indicated by the holdings of major herbaria and must be increasing yearly. A broad ecological amplitude has evidently enabled *Arthraxon hispidus* to spread and flourish widely since its introductions into the United States.

Selected Specimens of Taxonomic and/or Floristic Significance.

[Asterisk (*) indicates locations new since Chase's report (Hitchcock, 1950); at least one specimen from each county of the range is included, except for counties in the Carolinas newly reported by Radford et al. (1968) for which no specimens were seen; abbreviations of herbaria follow the recommendations of Lanjouw and Stafleu (1964).]

PENNSYLVANIA. *Bedford Co.: *Berkheimer* 17684 (GH, US). Philadelphia: *Scribner* s.n., n.d. (US 740269); *Scribner*, in 1878 (US); ***B??k*, in 1877, annotated by E. Hackel as *A. ciliaris* var. undet. (US); *Scribner* 86 (GH). MARYLAND. *Baltimore Co.: *Reed* 33143, see Reed (1965) (US). Montgomery Co.: *Benedict* 5440, with characters of var. *hispidus* (US); *Kiger* 209, 377, *near junction of Interstate Rts. 495 and 70-S (MARY, US); *Killip* 40187, this and *Benedict* 5440 are the only collections from the state prior to 1950 with the characters of var. *hispidus* and were the basis for Chase's report of that variety from Maryland (US); *Killip* 41388, collected from same general site as *Benedict* 5440 but four years later, somewhat depauperate looking, and with characters of var. *cryptatherus* (US); *Norton*, in 1940 (MARY); *Smith* 4918 (US). Prince Georges Co.: *Hermann* 11609 (US). DISTRICT OF COLUMBIA. *Allard* 11068 (GH); *Worthley*, in 1951 (US). VIRGINIA. *Albemarle Co.: *Davenport*, in 1959 (US). Alexandria: *Hotchkiss* 5560 (US). Arlington Co.: *Hermann* 9923 (GH) and *s.n.* on same date in 1938 (US); *Kiltz*, in 1960, *Ft. Myer (US). Elizabeth City Co.: *Fernald, Long & Fogg* 4758 (US). Fairfax Co.: *Chase* 12653 (US); *Fosberg* 30142 (US). Greensville Co.: *Fernald & Long* 13551 (GH). Sussex Co.: *Fernald & Long* 9517 (GH, US). NORTH CAROLINA. Brunswick Co.: *Blomquist* 4885 (GH). Guilford Co.: *McCrary*, in 1927 (US). Orange Co.: *Blomquist* 10946 (GH). *Rutherford Co.: *Blake* 12463 (US); *Freeman* 52484 (US). SOUTH CAROLINA. *Abbeville Co.: *Radford* 50846 (GH). Pickens Co.: *Newman*, in 1903 (US). GEORGIA. Cherokee Co.: *Duncan* 8926 (GH, US). *Clayton Co.: *Duncan* 10681 (US). Dawson Co.: *Duncan* 4290 (GH, US). *Elbert Co.: *Duncan* 10549 (US). *Floyd Co.: *Duncan* 13312 (GH). Troup Co.: *Young*, in 1922 (US). Walton Co.: *Duncan* 7893

(GH, US). FLORIDA. *Stokes*, in 1925 (US). *Gadsden or Liberty Co.: *Godfrey* 59971, at Aspalaga (GH). TENNESSEE. Anderson Co.: *Jennison* 3347 (US). Campbell Co.: *Underwood* 1373 (US). Montgomery Co.: **Clebsch*, in 1948 (US). ALABAMA. Auburn: "communicated by *G. Fick*," in 1929, but the state not included in Chase's 1950 report despite this specimen (US). *Talladega Co.: *Banks*, in 1959 (US). MISSOURI. St. Louis: *Steyermark*, in 1933 (US). ARKANSAS. Garland Co.: *Moore* 470156 (US); *Palmer* 24259 (GH); *Palmer* 26445 (US). Hot Springs Co.: *Hale* 2067 (US). *Montgomery Co.: *Demaree* 34326 (US). Washington Co.: *Demaree* 675 (US). LOUISIANA. *E. Feliciana Parish: *Thieret*, in 1965 (US). *Pointe Coupee Parish: *Thieret*, in 1964 (US). Richland Parish: *Silveus* 5395 (US). CULTIVATED. *Celarier*, in 1953, cultivated in nursery at Stillwater, Okla. from orig. coll. in District of Columbia (US). *Suksdorf* 5316, "raised from young plants collected on ballast at Portland, Oregon," evidently the sole basis both for Hitchcock's 1935 report from Oregon and for Chase's 1950 report from Washington (US).

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ADDITIONS TO THE FLORA OF THE BAHAMA ISLANDS

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During late December of 1968 I collected briefly on the Grand Bahama Island followed by a few days on Eleuthera till 2 January 1969. I returned to Eleuthera the following year and collected for about two weeks during the same December-January period. In total 204 taxa were found besides strictly cultivated plants, bryophytes and algae.

I was surprised on using the 50 year old Bahama Flora (Britton & Millspaugh, New York, 1920) to find that many of my collections represented plants new to the Bahamas and to either the Grand Bahama Island or to Eleuthera. These islands are among the largest in the archipelago, the first tragically undergoing heavy land development, the second of interest because of early settlement (1649) where garden escapes are common-place and often indistinguishable from the native vegetation. Little taxonomic research specific to the Bahamas has been attempted since the Flora, excepting a major contribution by Howard for the Bimini

[1]I appreciate the review of this manuscript by Dr. Richard A. Howard, Arnold Arboretum, Harvard University.

Island group (Ecol. Monogr. **20**: 317-349, 1950), and perhaps this inactivity accurately reflects the remarkable figure of 28 per cent of the vegetation which I shall report as occurring for the first time in the Bahama Islands or on one of the specific islands visited. This per cent assumes the Flora and Howard's paper as base lines.

Three genera are reported as new to the islands, namely, *Hedyotis (Houstonia)*, *Rhynchelytrum (Tricholaena)* and *Rotala*; additionally *Solidago* is new as a native or naturalized genus. Taxa are listed below in three groups: those new to the Bahama Islands followed by those new to the Grand Bahama Island and to Eleuthera. Numbers refer to my collections and are followed by one or more acronyms indicating place of deposit. A complete set of specimens is housed at the Missouri Botanical Garden.

Having excluded cultivated plants from my data I shall mention only several of the more interesting: on the Grand Bahama Island — *Sorghum coriaceum* Snowden (7178 — GH, MO, NY), *Vitex trifolia* L. var. *subtrisecta* (Kuntze) Moldenke (7124 — FTG, MO, W); and on Eleuthera — *Alternanthera williamsii* (Standley) Standley (7206 — FTG, MO), *Pentas lanceolata* (Forsk.) Deflers (7200 — FTG, MO, NY), and *Pilea serpyllifolia* Wedd. (7525 — FTG, GH, MO).

I. Plants Newly Reported for the Bahama Islands

BORAGINACEAE: *Heliotropium angiospermum* Murray: Eleuthera, 7183 (FTG, MO, NY, W).

COMPOSITAE

Flaveria bidentis (L.) O. Ktze.: Eleuthera, 7221 (GH, MO, NY, US).

Solidago sempervirens L.: Grand Bahama Island, 7171 (FTG, MO, NY). See Howard (Ecol. Monogr. 20: 349, 1950) who found the species cultivated in the Bimini Island group.

GENTIANACEAE: *Sabatia stellaris* Pursh: Eleuthera, 7190 (FTG, MO, NY).

GRAMINEAE: *Rhynchelytrum roseum* (Nees) Stapf & Hubb.: Eleuthera, 7230 (MO, US).

LYTHRACEAE: *Rotala ramosior* (L.) Koehne: Grand Bahama Island, 7113 (FSU, FTG, MO, NY, W).

PHYTOLACCACEAE: *Phytolacca purpurascens* A. Br. & Bouché: Grand Bahama Island, 7166 (FTG, MO, NY); see Nowicke (Ann. Missouri Bot. Gard. 55: 317. 1969).

RUBIACEAE

Hedyotis nigricans (Lam.) Fosb. var. *filifolia* (Chapm.) Shinners: Grand Bahama Island, 7182 (FSU, FTG, MO, NY, W).

Spermacoce cf. *aspera* Aublet: Eleuthera, 7201 (FTG, MO, NY, W).

VERBENACEAE: *Clerodendrum speciosissimum* Van Geert: Eleuthera, 7203 (FTG, MO). Verified by Dr. Harold N. Moldenke.

II. Plants Newly Reported for the Grand Bahama Island

AMARYLLIDACEAE: *Agave bahamana* Trelease: 7179 (FTG, MO, NY, W).

CASUARINACEAE: *Casuarina equisetifolia* Forst.: 7177 (FTG, MO, NY, W).

COMPOSITAE

Eupatorium odoratum L.: 7170 (FTG, MO, US, USF).

Flaveria linearis Lag.: 7175 (FTG, MO, US).

CYPERACEAE: *Cyperus ferax* L.: 7155 (FTG, MO, NY, W).

EUPHORBIACEAE: *Chamaesyce hirta* (L.) Millsp.: 7156 (FTG, MO, NY). Determined by Dr. Derek Burch.

GENTIANACEAE: *Eustoma exaltatum* (L.) Griseb.: 7158 (MO).

GRAMINEAE: *Uniola paniculata* L.: 7105 (GH, MO, SMU).

LEGUMINOSAE: *Cajanus cajan* (L.) Millsp. (as *Cajan cajan* (L.) Millsp.): 7126 (FTG, MO); 7129 (FTG, MO, NY, W).

MALVACEAE: *Sida carpinifolia* L.f.: 7147 (FTG, MO, NY, W).

OXALIDACEAE: *Oxalis corniculata* L. (as *Xanthoxalis corniculata* (L.) Small): 7123 (FTG, MO, NY). Determined by Dr. Duncan M. Porter.

POLYGONACEAE: *Coccoloba krugii* Lindau: 7154 (FTG, MO, NY, W). Verified by Dr. Richard A. Howard.

SCROPHULARIACEAE: *Capraria biflora* L.: 7145 (FTG, MO, NY, W).

III. Plants Newly Reported for Eleuthera

*Distribution from the Flora somewhat questionable, but probably does not include Eleuthera.

AMARANTHACEAE: *Amaranthus dubius* Mart.: 7521A (FTG, GH, MO).

BIGNONIACEAE: *Tecoma stans* (L.) H.B.K.: 7533 (FTG, GH, MO).

BOMBACACEAE: *Ceiba pentandra* (L.) Gaertn.: 7534 (FTG, GH, MO, USF).

COMPOSITAE

Aster bracei Britton: 7459 (FTG, MO, US, USF).

**Erigeron pusillus* Nutt. (as *Leptilon pusillum* (Nutt.) Britton): 7519 (FTG. GH, MO, USF).

Mikania scandens (L.) Willd.: 7465 (FTG, MO, NY, USF).

Vernonia cinerea (L.) Less.: 7223 (FTG, MO, US, USF).

CONVOLVULACEAE: *Ipomoea hederifolia* L. (as *Quamoclit coccinea* (L.) Moench): 7202 (FTG, MO, NY). Determined by Royce L. Oliver.

CYPERACEAE

Cladium jamaicense Crantz (as *Mariscus jamaicensis* (Crantz) Britton): 7491 (FTG, MO, NY, USF).

Cyperus ligularis L.: 7532 (MO, NY).

Dichromena colorata (L.) Hitchc.: 7468 (FTG, MO, NY, USF).

Eleocharis capitata (L.) R. Br.: 7458 (FTG, GH, MO, NY, USF).

EUPHORBIACEAE

**Phyllanthus caroliniensis* Walter subsp. *saxicola* (Small) Webster (as *P. pruinosus* Poeppig): 7472 (FTG, MO, USF).

**P. epiphyllanthus* L. (as *Xylophylla epiphyllanthus* (L.) Britton): 7208 (FTG, MO, NY, W).

Ricinus communis L.: 7537 (FTG, GH, MO, USF).

GENTIANACEAE: *Eustoma exaltatum* (L.) Griseb.: 7436 (FTG, MO, NY, USF).

GRAMINEAE

Chloris inflata Link (as *C. paraquaiensis* Steud.): 7229 (FTG, MO).

Setaria geniculata (Lam.) Beauv. (as *Chaetochloa geniculata* (Lam.) Millsp. & Chase): 7474 (FTG, MO).

LEGUMINOSAE

Crotalaria incana L.: 7228 (MO).

Parkinsonia aculeata L.: 7234 (FTG, MO, NY, W).

Poinciana regia Bojer (as *Delonix regia* (Bojer) Raf.): 7515 (FTG, MO).

Stylosanthes hamata (L.) Taubert: 7484 (MO, NY).

Tamarindus indica L.: 7462 (FTG, MO, NY).

LILIACEAE: *Sansevieria quineensis* Willd.: 7449 (FTG, GH, MO, USF).

MALVACEAE

Gossypium barbadense L.: 7447 (FAU, MO, NY); 7535 (FTG, GH, MO, USF).

Thespesia populnea (L.) Solander ex Corr.: 7509 (FTG, GH, MO).

OLEACEAE: *Jasminum azoricum* L.: 7501 (FTG, GH, MO, USF).

PASSIFLORACEAE: *Passiflora cupraea* L.: 7423 (FTG, GH, MO); 7514 (MO, USF).

RHAMNACEAE: *Gouania domingensis* L.: 7431 (FTG, MO, NY, USF).

SCROPHULARIACEAE: **Capraria biflora* L.: 7210 (FTG, MO, NY, W); 7444 (FAU, GH, MO, USF).

THEOPHRASTACEAE: *Jacquinia keyensis* Mez [not of the Flora which is *J. armillaris* Jacq. (*J. barbasco* Mez)]: 7460 (FTG, MO, NY, USF).

VERBENACEAE

Clerodendrum fragrans Vent. var. *pleniflorum* Schauer: 7499 (FTG, GH, MO).

Lantana balsamifera Britton: 7216 (FTG, MO, W). Determined by Dr. Harold N. Moldenke.

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A DEFENSE OF CAREX INTUMESCENS VAR. FERNALDII

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Recent manuals tend to dismiss *Carex intumescens* var. *fernaldii* Bailey as a northward cline in the species toward narrowed perygynia. Gleason (1952) merely mentions this, and in a later manual (1963) ignores it entirely. Radford, Ahles and Bell (1968) specifically submerge the variety. If only dimensions of perigynia were involved this would appear to be valid. There is, however, a style character not mentioned in these manuals, including that of Fernald (1950), who recognized varieties of *C. intumescens* on ancillary characters.

Prevailing descriptions of *C. intumescens* hold that the style throughout the species is straight or slightly contorted (arcuate would be more descriptive). In keying specimens I recently obtained from eastern Canada, I noticed that inside mature perigynia the achenes had styles which were more than arcuate. The lower half of the style executed a half- to complete coil on a horizontal, or near horizontal, plane, as does the style of *C. lupulina* Muhl. I found this generally true in specimens with ripe narrow perigynia from boreal eastern North America. More southerly plants, with wider perigynia, had the usual straight to arcuate (on a vertical plane) styles. Descriptions of the varieties, as I recognize them, follow:

Carex intumescens Rudge var. **intumescens**: The lustrous perigynia conic-ovoid, 5-8 mm. wide at widest point near base; achenes broadest near middle, acuminately rounded to tip; style of *mature* achene straight or vertically arcuate. Florida to Texas to Maine, Nova Scotia, southwest Quebec to Wisconsin. Rare or absent in boreal parts of the range, abundant southward.

Carex intumescens var. **fernaldii** Bailey: The lustrous perigynia lanceolate to lance-ovoid, 3-5 mm. wide at widest point near base; achenes broadest above middle, with a pronounced shoulder rounding abruptly to tip; style of *mature* achene with a half- to single distinct coil in basal

half. Newfoundland to Manitoba to northern and western New England, New York, and northern Pennsylvania, Michigan to Minnesota. Also in high mountains of Virginia and North Carolina. The prevailing variety in boreal eastern North America.

The prevailing keys treating sect. *Lupulinae* Tuckerm. use degree of style contortion, in part, to separate the first two groups of species in the section. With the style character of *C. intumescens* var. *fernaldii* redefined, the keys lose some dependability to separate this species. It is suggsted that reference to style character be dropped from the first legs of keys. Remaining characters are sufficient to separate the first two groups of species. Style character is more useful in succeeding legs of keys.

Until such time as transplant studies prove or disprove the constancy of style character of the varieties of *C. intumescens*, they should be recognized. Style contortion is probably a corollary of confinement imposed by perigynium sides, i.e., the narrower the perigynium, the more contortion might be expected. The biological significance and taxonomic value of the character of degree of style contortion in this and several other species of *Carex* requires experimental determination.

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A NEW COMBINATION IN TOFIELDIA GLUTINOSA (LILIACEAE)

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While reviewing the genus *Tofieldia* for the Intermountain Region of the western United States, I consulted the numerous specimens of the *T. glutinosa* complex deposited at the United States National Herbarium. Although none of the varieties of this complex is known to occur in the Intermountain Region, I did encounter a nomenclatural problem which ought to be resolved.

When Hitchcock (1944) reviewed *Tofieldia glutinosa* for western North America, he reduced *T. intermedia* to synonymy under his "ssp. *typica*," or what would now be called var. or ssp. *glutinosa*. In doing so, Hitchcock stated (page 494): "Rydberg cited, as the type of *T. intermedia*, a specimen from Sheh-Shock [sic] Lake, Alaska, collected in 1895, *M. W. Gorman* 78 (Type at the New York Botanical Garden). This specimen is in flower rather than fruit and it therefore cannot be ascertained whether or not the seeds would have a tight or loose testa — the only diagnostic character that will serve to distinguish ssp. *typica* from ssp. *brevistyla* in all cases. Nearly all collections from northern British Columbia have the testa characteristic of [*T.*] *glutinosa* [ssp.] *typica*, so it seems reasonable to assume that Rydberg's type may belong with that entity."

What seemed reasonable to assume with the limited material then available to Hitchcock now does not seem so, as all Alaskan specimens reviewed so far belong to Hitchcock's ssp. *brevistyla*. Likewise, fruiting specimens from near the type area of *Tofieldia intermedia* all exhibit the loose testa typical of ssp. *brevistyla*. Other specimens which range far to the north in Alaska (then unavailable to Hitchcock, due mainly to the Second World War) all belong to the latter taxon, a point apparently accepted by Hultén (1968) in his latest revision of the Alaskan flora.

As I prefer to recognize these entities at the varietal level (following Hitchcock, 1969), the following new combination is necessary:

Tofieldia glutinosa (Michx.) Pers. var. **intermedia** (Rydb.) Reveal, comb. nov., based on *T. intermedia* Rydb., Bull. Torrey Bot. Club 27: 528. 1900. (*Gorman* 78, Sheh-shooh Lakes, Alaska, in 1895, holotype at NY, isotype at US!).

Triantha intermedia (Rydb.) Gates, J. Linn. Soc., Bot. 44: 137. 1918.

Tofieldia occidentalis S. Wats. var. *intermedia* (Rydb.) Peck, Manual High. Pl. Oregon 189. 1941 and Madroño 6: 133. 1941.

Tofieldia glutinosa (Michx.) Pers. ssp. *brevistyla* C. L. Hitchc., Amer. Midl. Naturalist 31: 495. 1944. (*Hitchcock & Martin* 1731, Blackwater Lake, about 32 miles north of Golden, British Columbia, Canada, 11 July 1941, holotype at WTU, isotype at NY!).

T. glutinosa var. *brevistyla* (C. L. Hitchc.) C. L. Hitchc., Univ. Wash. Publ. Biol. 17(1): 806. 1969.

Work on the Intermountain Flora is supported, in part, by my N.S.F. Grant, GB-22645.

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SEVENTY-FIVE YEARS LATER, A SECOND STATION IN NEW ENGLAND FOR MICRASTERIAS NORDSTEDTIANA

L. C. Colt, Jr. and C. Barre Hellquist

In the year 1895 L. N. Johnson reported finding the rare desmid *Micrasterias Nordstedtiana* Wolle in Meredith, Belknap County, New Hampshire. This report from the Granite State is apparently the only previous one of this desmid within the New England region, and one of the very few from the United States.

In addition to the original citation by Wolle (1884), G. M. Smith (1921) lists it among the phytoplankton of the inland lakes of Wisconsin, but in only one lake.

Collections of *Proserpinacea palustris* L. from Icehouse Pond, located a long half-mile from Interstate Route 495 on West Main Street in Hopkinton, Norfolk County, Massachusetts, yielded a very rich collection of algae which are being reported on at another time. In the material of the collection the authors found several specimens of this desmid of rather simple form. Figure 1a is redrawn from the camera lucida drawing by the first author. Figure 1b shows the neck prominences of the type described by Wolle, and 1c shows the semicell of the specimen found by Johnson. Both 1b and 1c were redrawn from plates in the publications by those authors.

Johnson noted that his specimen varied from the type in that the lobes terminated in two spines rather than the three or more figured by Wolle, and that the projections on the sides of the neck ended in two spines, rather than being the short conical prominences of Wolle's figure. Comparing the two figures, one suggests that Johnson somewhat understated the differences.

Our specimen compares very favorably to the type, except that ours also shows but two spines at the end of each polar lobe, rather than the three or four indicated by Wolle.

With the single findings by Johnson and Smith, and the two reported by Wolle (1892), one each in New Jersey and

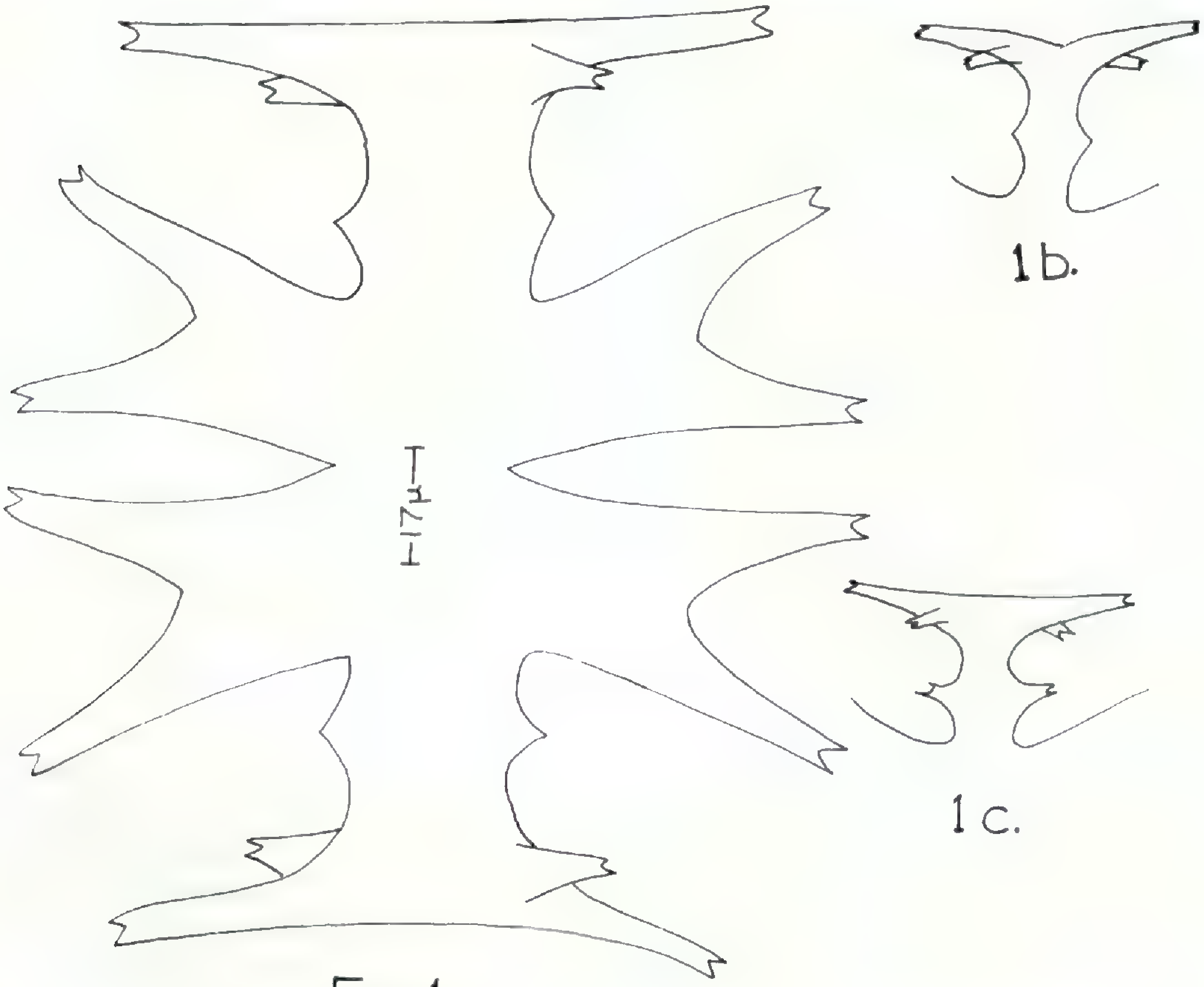

Fig. 1a.

Fig. 1. *Micrasterias Nordstedtiana* Wolle. 1a, *Colt & Hellquist*, Hopkinton, Massachusetts, scale is indicated. 1b, type specimen from Wolle (1884). 1c, from Johnson (1895). 1b & 1c not drawn to scale.

Pennsylvania, our station appears to be only the fifth in the United States. As the illustration shows, the striking simplicity of the desmid makes identification easy once it appears under the microscope.

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VASCULAR PLANTS NEW TO NORTH DAKOTA: As the result of fieldwork done in North Dakota by members of the North Dakota State University botany staff and the Kansas University botany staff during 1967-1969, seven new vascular plant records were recorded. These are as follows:

Equisetum palustre L. was found growing in a boggy area along the shore of the Sheyenne River 16 miles east and 5 miles north of Lisbon, Ransom County, North Dakota, on July 6, 1969. (*Ralph Brooks* 1554, NDA.) Moore and Tryon (1946) list this species for Minnesota. This record represents a western extension of distribution.

Eragrostis spectabilis (Pursh) Steud. was found growing in a sandy, native prairie 3 miles east and 6.5 miles north of McLeod, Ransom County, North Dakota, on August 7, 1969. (*William T. Barker* 6147, NDA.) This species is common in the western tier of Minnesota counties bordering North Dakota, but this is the first record of the species west of the Red River.

Berberis repens Lindl. was found growing in scattered colonies under *Juniperus scopulorum* Sarg. in clay soil in Sec. 32, T 130 N. R 106 W, Bowman County, North Dakota, on August 26, 1969. (*Don Hoag*, NDA.) Winter and Van Bruggen (1959) record this species for Harding County, South Dakota. The North Dakota station for this species is six miles north of Harding County, South Dakota.

Gaura parviflora Dougl. was found growing in a prairie railroad right-of-way 7 miles east of Sentinel Butte, Golden Valley, North Dakota, on July 23, 1969. (*N. Zaczkowski* 1180, NDA.) This species is found in disturbed and waste places throughout Montana and South Dakota. It is known from only this station in North Dakota.

Halenia deflexa (Sm.) Griseb. was found growing in a boggy wooded area 5 miles north of Mountain, Pembina County, North Dakota, on July 25, 1967. (*H. A. Stephens* 14760, KANU.) Moore and Tryon (1946) list this species for

Minnesota. This record represents a western extension of distribution.

Penstemon procerus Dougl. was found growing in a prairie roadside ditch 1/2 mile east of Northgate, Burke County, North Dakota, on June 20, 1969. (*Glen D. Hegstad* 2410, NDA.) Scoggan (1957) reports this species for Manitoba, Canada and Booth and Wright (1966) record this species from the western two-thirds of Montana. The North Dakota record probably represents a southern extension of distribution.

Thelesperma marginatum Rydb. was found growing in a sandy prairie area, 5 miles west and 2 miles north of Fortuna, Divide County, North Dakota, on June 10, 1969. (*Glen D. Hegstad* 3887, NDA.) Booth and Wright (1966) record this species for McConen County, Montana, so the North Dakota record represents an eastern extension of distribution.

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RECORDS ON THE FLORA OF WISCONSIN: **Satureja Acinos** (L.) Scheele (Labiatae) is a somewhat weedy species, adventive from Europe (treated as *Acinos arvensis* (Lam.) Dandy in Clapham, Tutin, and Warburg, Flora of the British Isles, second edition, 1962, p. 743) and reported to range from southwestern Quebec and southern Ontario to New England to Michigan and New Jersey. This is to report an extension of its range into extreme northeastern Wisconsin: Marinette County, sunny edge of road through sandy woods at Chalk Hills Girl Scout Camp, several hundred yards west of the Menominee River bank, section 19, T35N, R22E, Amberg Township, *Harriman* 5709, 20 June 1970. Two such specimens are deposited in the herbarium, Wisconsin State University-Oshkosh, and a duplicate has been sent to WIS, where Dr. Hugh Iltis has kindly confirmed my identification. In addition, the plant was found at the edge of a gravel pit, half a mile distant from the first site, *Harriman* 5627. Two sheets of this second collection are also deposited here. In both places, the plant occurred abundantly, suggesting that it was introduced some time ago.

Since the collections were made only a few hundred yards from the Menominee River, the Michigan-Wisconsin border at that point, it at first appeared that this was a trivial range extension. But inquiry to Dr. Rogers McVaugh, MICH, revealed that the plant is known from the Upper Peninsula of Michigan only in Mackinac County — the collections reported here extend the plant's known range some 200 miles west. I searched unsuccessfully for the plant in likely habitats in Menominee County, Michigan, just to the east of Marinette County. R. C. Koeppen (1957. Preliminary Reports on the Flora of Wisconsin. No. 41. Labiatae — Mint Family. Trans. Wis. Acad. Sci., Arts and Letters. **46**: 115-140.) does not report the plant for Wisconsin, nor are there any records for the plant in Wisconsin at WIS.

Holcus lanatus L. was discovered in a sandy, newly seeded roadside ditch on Cobb Town Road at U.S. 10, 0.6 mile east of the Waupaca River, section 22, R11E, T22N, Farm-

ington Township, Waupaca County, Wisconsin. First collections were made 27 June 1970 (*Harriman* 5789, deposited in the herbarium. Wisconsin State University — Oshkosh) of plants in flower. Numerous other plants were found in fruit at the same site on 4 July 1970 (*Harriman* 5956, deposited as above, with a duplicate of this latter collection sent to WIS, where Dr. Hugh Iltis kindly confirmed my identification). According to Dr. Iltis, WIS had no specimens of the plant for Wisconsin; Dr. Emil Kruschke at MIL likewise informed me there were no Wisconsin records for the plant there. The plant is not shown for Wisconsin in Fassett (Grasses of Wisconsin, 1951) nor in Hitchcock & Chase (Manual of the Grasses of the United States, 1950); Fernald (Gray's Manual, 8th Edition, 1950) does not include Wisconsin in the known range of the plant.

Festuca myuros L. is included in the Wisconsin flora by the authorities cited above, based on a single specimen collected in 1914 (*Charles Goessel* 30440, Sheboygan, Wisconsin, 11 August 1914; in MIL). There are no other Wisconsin records for the plant deposited there, nor at WIS. I collected numerous plants in a shaded, limestone gravel driveway at 5188 Bittersweet Lane, section 30, R17E, T19N, Oshkosh Township, Winnebago County, Wisconsin, 26 June 1970, *Harriman s.n.* Vouchers are deposited in the herbarium, Wisconsin State University — Oshkosh, and at WIS, where Dr. Iltis confirmd my identification.

Both of these grasses appear to be accidental introductions, perhaps as contaminants in grass seed; they may in the future become fully naturalized in the state.

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NON-ADDITIVE CULTURES FOR ALGAE

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Phycological literature is replete with a variety of techniques for the handling of algae once they have been collected. Aside from the rather obvious requirement for examination of the living material as expeditiously as possible, one might then choose from a variety of methods such as are found in Smith (1950), Pringsheim (1946a, 1946b), or Prescott (1954). The goal of the investigator certainly suggests the proper method or methods to be used. During several years of collecting fresh-water algae from a variety of localities in New England, this author has utilized a method that is much less sophisticated than those usually employed, yet as a result, has been able to achieve a greater than usual use of the material. It is the purpose of the author to present a brief discussion of the technique and the use that may be made of it.

The collections by the author, principally in the towns of Medfield, Walpole, and Sharon, all within the area of Norfolk County, Massachusetts, have been attempts to isolate causes of and mechanisms for algal periodicity. Standard techniques of collection have been utilized, and whenever possible or practical, at least two methods of preservation of representative specimens. More often than not, considerable quantities of material were left after initial use and it is this extra material which has been the source of much interest and work.

The method employed is simplicity in itself. The wide-mouthed jar with the remaining material was tightly capped with a Bakelite cap, and placed on a window shelf with a southwesterly exposure. The window is shaded by a rather dense stand of Eastern White Pine (*Pinus Strobus* L.) and gets direct sunlight only during the latter part of the afternoon. The material in the jars is not monitored critically on an exacting or rigid schedule, rather, casual observations are used to check on the material within the jars, with

detailed examination given to those that exhibit distinct changes in the material.

Gilbert Smith (1950), in a discussion of the techniques and problems of culturing algae makes several points that seem appropriate to mention here. He suggests that "there is no general method by which collections of algae may be kept alive in the laboratory for indefinite periods"; and that "algae maintained alive under laboratory conditions so frequently develop abnormal thalli that one should compare the laboratory-grown algae with freshly gathered specimens to avoid misleading conclusions." Finally he makes the point that, because the new environment favors the growth of only certain of the algae within the culture, changes in the structure of the association, are to be expected particularly in regard to the relative numbers of each species that are present.

It is the opinion of this author that Smith's initial premise is not valid for all conditions of culture. He does suggest that water from the original habitat is often the best culture solution, a fact that this investigator has also found to be the case. However, based on the experience with cultures in the author's own laboratory it is entirely possible to hold algal cultures in a fresh, useful condition for more than a year. It might indeed be possible to hold them for longer periods than that. A number of jars now on the shelves have been there for that period and as of now show no signs of deterioration.

Similarly the investigations leading to this paper do not entirely support the premise that abnormalities are to be commonly encountered. Obviously the particular species, or even the genera used, may have a considerable bearing on this point. The only material that this author found dealing with algal abnormalities (Cushman, 1904) dealt with abnormalities that occur during division and following ingestion by crustaceans. As species were encountered in the cultures under discussion careful measurement against published standards (e.g. Prescott, 1962), suggests that abnor-

malities are extremely rare. Only one instance was found in this case, and it was deemed to be of no significance, as will be shown later.

Smith's third premise, that the numbers of each species change because of the changed environment, is held to be entirely valid, and as a matter of fact, is one of the most desirable attributes to this method of culture. As the conditions within the jar change, the response by the algae yields quite a different association, often involving the loss of one or more of the original forms, and the emerging of others as dominants. The most obvious variable in the present case is that of temperature. The original habitats having not only greater extremes, but due to changing environmental conditions consistent with seasonal change, quite different averages. The two different cultures used as illustrations in this paper, for example, have had temperatures with extremes of 15° C, to 32° C, although the general average has run between 20-24° C, as might be expected within a house under normal conditions of living. The close proximity to the window glass accounts for the greater extremes.

One of the sets of material has been "on the shelf" since April of 1969. Two jars, quite different in original collection material, comprise one set. Both jars were collected from the same stream pool, at the same time, under the same conditions. One jar (Jar A hereafter) held *Tetraspora lubrica* (Roth) C. C. Agardh, with a small amount of dead grass stems, and a like amount of *Fontinalis* (*Fontinalis gigantea* Sulliv.), a rather common aquatic moss in this region. As might be expected the abnormally warmer environment led to the complete destruction of the *Tetraspora,* a species that is usually a cold-water type. The second jar, collected from a point that was slightly more in midstream than the former jar, contained a quantity of *Fontinalis,* to which was attached a small amount of *Tetraspora,* and a considerable quantity of *Microspora amoena* (Kuetz.) Rabenhorst. This second jar is Jar B, for the purposes of this discussion.

Casual examination of both jars in late February of 1970 revealed a considerable change. Jar A now showed as a dominant form *Nitella*, which close examination showed to be *N. flexilis* (L.) C. A. Agardh. Jar B also had *Nitella* as a prominent species, but an even greater growth of *Vaucheria geminata* (Vauch.) De Candolle. The *Nitella* in each jar was not found in the initial examination of the material in 1969, hence it must be assumed that the original collection included reproductive bodies in some form. The *Vaucheria* might easily have been missed among the *Fontinalis*, if as is suspected, it existed in rather minute amounts in the original material.

Jar A contained no other filamentous or multicellular alagae, but the surface of the *Nitella* was crowded with epiphytic species. The four most numerous species being *Characiopsis longipes* (Rabenh.) Brozi, *Characium pringsheimii* A. Braun, *C. ornithocephalum* A. Braun, and *C. rostratum* Reinhard. The most common species represented in the detritus on the bottom of the jar was *Pleurotaenium ehrenbergii* (Breb.) De Bary. This species was not found in the living state, however, the identification was made from semi-cells in the litter.

Jar B contained an abundance of the filaments of *Hyalotheca dissiliens* (Smith) De Brebisson, and one species of *Oedogonium* which had not developed the reproductive structures requisite for precise identification. In addition, several other desmids were common: *Closterium leibleinii* Kuetzing being the most abundant, while *C. ehrenbergii* Meneghini and *Euastrum affine* Ralfs were encountered less frequently.

Earlier mention was made of one species that did not conform to the published size ranges for it. This species was *Microspora amoena* (Kuetz.) Rabenhorst, and it showed to be larger than normal by some 3 microns in both length and diameter. It otherwise met all the required taxonomic characteristics and was assigned by this investigator to that species, especially as it had been identified in the original collection, and at that time no characters were

unusual. This seems to be the sort of situation described by Smith, but whether or not it is as widespread as he seemed to think is open to question.

Neither of the jars examined in 1970 showed many motile algae, and this circumstance agrees with Smith, his suggestion being that this type went first in culture and should be sought for first in examination of material. Two species were found infrequently in Jar B. *Eudorina elegans* Ehrenberg and *Synura uvella* Ehrenberg were among the strands of material in that jar.

While the previous example consisted of members of the Chlorophyta, the presence of species of Cyanophyta, for example, can be shown as easily. A collection from a small, slow, feeder stream in the same general locality, cultured from March of 1969 and lately examined, revealed a considerable quantity of *Hapalosiphon hibernicus* West & West, both as part of an association forming a mat on the surface of the water in the jar, and entangled down in the jar among the other filaments. The other member of the surface mat was a species of *Anabaena* which lacked sufficient taxonomic characters to identify the species.

This culture was and is well-filled, it being impossible to look clear through the jar. A large part of this dense mass was composed of *Fontinalis*, and the remainder partly filamentous Chlorophyta and partly detritus. The experience of this investigator has been that the genus *Microspora* is one of the most abundantly represented in most collections, at least within the Neponset River watershed. In addition to the filamentous desmid *Hyalotheca dissiliens*, three species of *Microspora*, *M. quadrata* Hazen, *M. stagnorum* (Kuetz.) Lagerheim, and *M. pachyderma* (Wille) Lagerheim made up the bulk of the filamentous material.

One last example to show the versatility of the method can be taken from a culture collected from a small, but deep and swiftly moving stream area considerably upstream from the other sites. The original material was collected from twigs and other vegetative debris hanging in the stream. The original material was primarily *Tetraspora lubrica*, but found among the specimens was *Rhizoclonium*

hieroglyphicum (Ag.) Kuetzing, *Pandorina morum* (Mueller) Bory, three clearly separate species of *Spirogyra*, one species of *Mougeotia*, and several strands of *Microspora amoena*.

Unlike the earlier examples, the long period prior to re-examination was not required in this instance. Two months after the "on the shelf" routine started, this investigator was able to isolate *Spirogyra denticulata* Transeau as one of three previously unidentified types. By contrast, one of the other species of *Spirogyra* had all but vanished.

On the basis of his experience with this rather simple method of algal culture this investigator is very much satisfied with the results that can be obtained. Not only can a much more representative grouping of the algae from a given station be obtained with patience and care, but very little time is required for maintenance.

One other advantage can be realized by the investigator who has the opportunity to work with students at almost any level. These mixed cultures provide an interesting challenge for the student and the teacher together, and as this writer has found, often open the channels of communication much more quickly than the uni-algal, more stereotyped material that is frequently encountered. Then too it frees the instructor from the problems of institutional orders and commercial suppliers, no small matter in this day of crowded schedules and classrooms.

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BOOK REVIEW

THE FLORA OF VERMONT[1]

Much of what the reviewer might say of this new edition of "The Flora of Vermont" can be found in his review of "The Flora of New England" (Rhodora 72: 137-141, 1970). In major part the present treatment consists of material, pertaining to Vermont, extracted from the larger work. In respect to the illustrations however which were badly reproduced in the earlier book, much care has been taken and they now are of good quality throughout. Also some illustrations have been added, — spikelets of *Trisetum*, fruits of *Ulmus*, plants of *Arceuthobium*, an inflorescence of *Rumex verticillatus* and leaves and bases of *Antennaria* spp.

In a few instances where several species were grouped together on a page in "The Flora of New England" these pages have been taken over without change in the present work even when, as in the willows, some species do not occur in Vermont. Thus there are illustrations in "The Flora of Vermont" of the following species which are not listed in the text as occurring in that State, *Salix pentandra, S. cordata, S. herbacea, S. arctophila, S. arygrocarpa, S. coactilis, S. glaucophylloides, S. cinerea, S. viminalis* and *S. Eleagnos.* Although it may be helpful to some Vermont botanists to have photographs of leaves of many extra-territorial species of willows at hand for purposes of comparison it might also lead to confusion. Some indeed might be led to believe that all of these exotics are bona fide residents of Vermont. The same inconsistency, if it may be called that, holds for the genus *Crataegus* where again the seven pages of illustrations of the thirty eight species that Seymour recognized in all New England, have been trans-

[1]The Flora of Vermont. A manual for the identification of all vascular plants including ferns and flowering plants growing without cultivation in Vermont, fourth edition. Agricultural Station Bulletin 660, the University of Vermont, Burlington, Vermont, 1969 ix + 393 pp. illus.

planted over into the Vermont book. Since, for Vermont, Seymour admits only thirty species, there are eight illustrated species that really don't belong. This admittedly is only one of many frustrations that will arise anyway in the identification of *Crataegus*. However because many of the illustrations were photographs taken of type material, Seymour's handling of this difficult group may be a step forward in clarifying the local species.

Though this reviewer can find no mention of the fact in the several pages of introductory material, it is quite apparent that the Vermont Flora has been taken pretty much out of the earlier "Flora of New England". Except for the convenience of a smaller book (393 as against 596 pages) the greater ease of finding one's way to information about Vermont and the lower purchase price one might therefore argue that the volume should have been delayed for a few years until the investigation of the Vermont flora stimulated by the publication of the New England Flora had resulted in so much new information that a Vermont treatment would be indeed a scientific contribution in itself. Actually however there are many minor changes throughout — additional townships or counties recorded for example and on pages 382 and 383 a considerable list of additions and corrections of which the reader should be aware. Considerable help in the refinement of data was given by Prof. W. Countryman and the late Leopold Charette whose help is duly acknowledged by the author. The final result is therefore considerably improved over the Vermont material in "The New England Flora".

Some effects of haste are to be noted. It should be unnecessary to repeat Vt. for each taxon each time localities of collections are given. In the genus *Betula* there is apparently an omission of *B. borealis* from that part of the treatment which deals with locality data although the species is given in the key. Also there is some mixup in the numbers assigned to the species in the key and farther along in the treatment of *Betula*.

Nomenclatural changes made in the "Flora" are given on page 382. It was the strict policy of Professor M. L. Fernald to publish nomenclatural changes in Rhodora rather than in a "manual". This was done before the 7th and 8th editions of Gray's Manual appeared. Although indexing is now better perfected and there is certainly less chance of missing such changes it would still be better communication to publish this kind of material in a Journal.

A final criticism should be made that has nothing to do with the body of the work. However on p. v of the Introduction there are some entirely misleading and incorrect statistics provided by means of which Mr. Seymour demonstrates that Vermont supports nearly five times as much variety as New England as a whole. It isn't necessary for an able taxonomist to be a competent statistician but someone should have caught this before it got into print. The same application of logic could be used to show that any area much smaller than New England would have greater variety than New England as a whole. Already certain persons in Vermont's sister state of New Hampshire are disturbed about the faulty line of reasoning. Actually New Hampshire with nearly the same area as Vermont probably has about as many species and therefore also by the formula given on p. v would have five times as much variety as New England as a whole. The only fair comparison, of course, would be to rate Vermont against other areas of about equal size. In any event it isn't likely that any other part of New England will permit Mr. Seymour for very long to escape with such a patent error.

The Flora of Vermont is a scholarly taxonomic work and will have value in educational institutions where students are made aware of its shortcomings and should, of course, find its way into the hands of anyone interested in the plants of Vermont. As a source of information about Vermont flora it is a major step forward from the 3rd edition. Indeed it was the demand for a new edition which hurried the publication of the present work.

One final word about New England State Floras. There is available at present a flora of New England. It is a very valuable and useful book and satisfies a long felt need though it may have some inadequacies in terms of providing information at the state level. There is a drive on at present to prepare new state floras within the New England area sparked by the Seymour Vermont Flora. Writing as a scientifically oriented critic this reviewer urges any who are planning such ventures to go well beyond the Seymour pattern in providing detailed information which will be of use to scholars aand scientists. This is not said to disparage the present flora but only to promote improvement.

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THE SYSTEMATICS AND ECOLOGY OF POISON-IVY AND THE POISON-OAKS (TOXICODENDRON, ANACARDIACEAE)[1]

WILLIAM T. GILLIS

INTRODUCTION

An ecological study in which I attempted to germinate seeds of poison-ivy was the forerunner of the present monograph. A study of the literature at that time revealed much confusion as to the application of names to the poison-ivy and poison-oak taxa, not to mention matters relating to its toxicity to man. Thus it appeared that *Toxicodendron* was deserving of a full-scale systematic investigation, even though it had been revised by Barkley (1937). Two of the three sections of the genus are treated herein, section *Venenata* being considered too large and diverse a group to include at the present time.

Barkley (ibid.) provided a taxonomic treatment of poison-ivy and the poison-oaks as part of a larger work on *Rhus* *(sensu lato)* in North America. His investigation was based chiefly on herbarium material, whereas this one has placed equal emphasis upon field and herbarium studies with a few laboratory experiments where appropriate. Because of the restriction of this investigation to a small segment of what Dr. Barkley monographed, it has been possible to examine the biology, natural history, and ecology of the taxa to a greater extent than he was able to do.

A number of problems had to be confronted in the course of this investigation. The plants are notoriously poisonous to man. The literature relating to *Toxicodendron* is voluminous partly because of its economic importance. The complex includes the most widespread taxa (in terms of native range) within the Anacardiaceae. It is further com-

[1]Submitted to the Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

plicated by its extreme plasticity. Whereas the leaf and fruit morphology is highly variable, the flower morphology is very conservative. The woody habit and dioecious nature of the taxa complicates experimental studies since at least three years are required for an individual to reach flowering stage from seed. Moreover, in most populations, it is not possible to determine the sex of an individual until it flowers.

Variants have previously been treated as species, subspecies, varieties, or forms without a unifying philosophy or concept of these taxonomic units. Often many of the characters used in differentiating taxa have been inconstant, and combined with one another in various ways, without consideration of the total variation of the plants in nature. Some of the characters which have been used would segregate plants within a single clone into several taxa. Misinterpretation and fractionation of species in the past have been due in part to incomplete knowledge of the range of variation and therefore little concept of which characters were useful taxonomically.

The position of *Toxicodendron* in the tribe Rhoeae is a fortunate one from the standpoint of understanding related genera. If a guide to the variability of plants in this tribe can be found in *Toxicodendron,* then the groundwork has been laid for future study of such vexing genera as *Rhus* and its segregates *Searsia, Melanococca,* and *Lobadium, Comocladia,* and indeed for investigation of the third section of *Toxicodendron,* section *Venenata.*

The present study brings together as much information about *Toxicodendron* (except section *Venenata*) as is now available. It is hoped that this monograph will contribute to a better comprehension of the plants for botanists and for those non-botanists who have need to understand them.

All taxa except *Toxicodendron radicans* subsp. *hispidum, T. nodosum, T. borneense* and *T. magnifolium* were studied in the field, but not all could be investigated with the same intensity. Although I had a considerably larger number of

specimens at my disposal than did Barkley (1937) and, in addition, benefitted from field experience with the plants, various problems remain for future exploration. If this investigation can serve as a reference point for study of problems in population variability, plant migration, modification through evolution, and variability in human sensitivity, then a primary objective will have been met.

ACKNOWLEDGMENTS

This monograph could not have been completed without the aid of a number of persons. I am sincerely grateful to many persons for their contribution. The patience, guidance, understanding, and friendship of Dr. John H. Beaman, my major professor, has contributed much to this study. He provided numerous suggestions which aided in the research and writing of the paper, and his help in obtaining funds and facilities for the investigation has been invaluable. He was also co-principal investigator under terms of the grant funded by the National Institutes of Health which supported a part of this research. Drs. John E. Cantlon, Jonathan Wright, Eugene Whiteside, Robert Bandurski, and John I. McClurkin, Jr., and Mr. Jerold Grashoff made helpful comments and criticisms concerning the manuscript.

Several persons took time to guide me in the field to find specimens in places not familiar to me: Dr. Edward G. Voss in parts of Michigan, Dr. H. G. Baker in California, Dr. Tetsuo Koyama in central Japan, Dr. T. Tsujii in northern Japan, Dr. Frank Craighead in southern Florida, Brother Daniel Lynch in Texas, and Dr. Barton Warnock in southwestern Texas. Others who assisted me when in the field were: Dr. Daniel B. Ward and the late Erdman West of the University of Florida, Mr. Jack Patterson of Nassau, Bahamas, Mr. John Verdier of Island Beach State Park, New Jersey, Dr. and Mrs. N. H. Haack of Haren, the Netherlands, M. and Mme. Henri Paillet of Paris, France, and Dr. and Mrs. Laurence Jones of Bedford, England.

Dr. Roland L. Fischer collected a larval form of *Arge* living on poison-ivy plants and provided determinations of insects known to visit poison-ivy.

Several persons sent me specimens for study: Dr. William Harlow, Dr. J. R. Griffin, Dr. Rollin Baker, Mr. Julian P. Donahue, Mr. Delzie Demaree, Dr. John Thieret, Dr. Robert Godfrey, Dr. D. C. D. deJong, Dr. Warren P. Stoutamire, Mrs. L. Kuprianova of Leningrad, Mr. I. W. Hughes of Bermuda, Dr. Tang-shui Liu of National Taiwan University, and Mr. J. A. R. Anderson of Kuching, Sarawak.

Translations were graciously provided by the following persons: Dr. Mladin Kabalin (Czech), Mr. Peter Khochta and Mr. Robert Parent (Russian), Dr. D. C. D. deJong (Dutch), and Dr. Shigeo Imamura (Japanese).

Of special assistance were those young men who accompanied me in the field and labored with me in gathering data: Messrs. Robert Tinker, Bruce McKenzie, Thomas Hicks, Wyn Wiksell, Edward Davis, Richard Steinhelper, and David Steensma.

I wish to thank the curators of the herbaria from which specimens have been used. These herbaria are listed at the beginning of the taxonomic treatment. Special thanks go to Drs. Robert McIntosh and Lloyd Shinners for exchanging isotype material with Michigan State University for my special study, and to Dr. Rogers McVaugh for duplicates of H. N. Bartlett collections.

Special thanks to Dr. Gordon Sabine, Vice President for Special Projects at Michigan State University for his inspiration and assistance throughout this project, often financial. Without the moral support of my late parents and my sister, Elizabeth G. Kohler, and of my colleagues among the graduate students in the Department of Botany and Plant Pathology, many of the ideas of this paper might not have matured.

A generous grant from the National Institutes of Health (No. C-3700) underwrote much of the field and laboratory work accomplished in connection with this research, and is gratefully acknowledged.

ECONOMIC SIGNIFICANCE

The chief importance of members of the poison-ivy complex to man is the dermatitis they cause. More than 350,000 cases of poison-ivy dermatitis are estimated for the United States per year (Turner, 1947). This averaged 2.5 cases per 1,000 persons, 17.7% of which were bed cases (averaging 3.5 days in bed), with 1.7 days of disability, 71.9% attended by professional medical personnel. Of economic impact are the 600,000 man-days of time lost from gainful employment due to the dermatitis and its complications. According to the California State Compensation Insurance Fund, Western poison-oak is the only weed in the state which is responsible for occupational injury (Jones, 1955). Statistics for that state, collected by the Department of Industrial Relations, indicate for 1953 that there were 3,658 cases reported as industrially incurred. Jones (ibid.) estimates the economic loss due to poison-oak dermatitis throughout California as $160,000 per annum. Extrapolation to other states of the Union where *Toxicodendron* species are found is not possible based on these figures alone, due to the differential in distribution of plant and of human population density, but such figures as those above suggest an enormous loss of gainful work by employees, not to mention personal misery, due to these plants.

From a medical viewpoint, members of this complex have had a colorful history. Some of the earliest works on record include a thesis submitted to the Medical Faculty of the University of Pennsylvania by Horsfield (1788), and later, one in Germany by Burse (1811). The reports in the medical literature during the nineteenth and twentieth centuries are legion, many of the significant ones summarized by Rostenburg (1955) and Kligman (1958). A homeopathic approach was prepared by Delestinne (1956), and other summaries of our modern medical knowledge by Epstein (1958). Bewildering and awesome are the lists of "treatments" which Kligman cites as having been used as topical therapy:

"Qualitatively, they range from the preposterous to the fantastic . . . A brief listing of some of the more interesting agents which have been thought beneficial clearly reveals the profound emotional effects of therapeutic desperation: morphine (topically!), bromine, kerosene, gunpowder (the symbolism here is beautiful), . . . aqua regia (!), buttermilk, cream and marshmallows (!) . . . strychnine (!), etc."

To this, I must add the preposterous idea of drinking a pint of photographers' hypo! Kligman continues:

"Throughout, there is a remarkable disregard for a simple biological fact, namely, that poison-ivy dermatitis is a self-resolving process."

In recent years, there have been attempts to cure or prevent the dermatitis by use of injections or preparations taken by mouth of a number of extracts of the poison under such trade names as Ivyol and Aqua Ivy (Howell, 1947; Passenger, Spain, and Strauss, 1956; and Gaillard, 1967). Dr. Kligman (ibid.) comments on these:

"One is confronted with the quixotic fact that many physicians achieved remarkable results with an extract biologically equivalent to water!"

Currently a study of oral prophylaxis is under investigation at the University of Cincinnati under the direction of Dr. Leon Goldman.

The disease mechanism is basically a delayed hypersensitivity of the contact variety, and is induced by simple molecular weight haptens rather than proteinaceous antigens (Crowle, 1964). A sensitizing antigenic complex is presumably created between the poison (3-*n* pentadecylcatechol) and skin proteins. The antigens thus are believed to be chemically-altered autologous skin proteins.

Aside from the medical aspects of the poisoning, poison-ivy *(Toxicodendron radicans)* has had other economic significances. Unbelievable as it may seem, poison-ivy has been cultivated in gardens in New South Wales, Australia (Anonymous, 1908), and in Dunedin, New Zealand (Connor, 1951), and sold as an ornamental by English nurserymen (Anonymous, 1949), probably as far back as 1640 (Miller and Martyn, 1807).[2] It seems to possess certain

[2]This is not to be confused with another plant called poison-ivy in Western Australia which is *Tinospora smilacina* Benth. (Menispermaceae) (Gardner and Bennetts, 1956).

horticultural values: (1) it has characteristics for the plant connoisseur who likes its autumnal foliage; (2) its autumn leaves have been used to highlight displays of fruit at shows; and (3) it is reported not to escape cultivation (!). Since 1919, poison-ivy has been planted along the dikes of Southwest Friesland Province in the Netherlands in an effort at dike consolidation. One colony has become established along more than 500 meters of one dike (Van der Ploeg, 1966).

Toxicodendron diversilobum is occasionally browsed by horses and cattle without apparent ill effects (Rostenburg, 1955a). Many birds, especially quail, feed on its fruits. Bees are reported to make honey from its flowers, an apparent non-toxic variety (Rostenburg, 1955b). Martin, *et al.* (1951) list a number of birds which eat poison-ivy and poison-oak fruits (not specifying the scientific names for either of the plants they had in mind), particularly in winter when other foods are scarce. Among 55 listed bird species which have been observed eating the seeds, yellow-shafted flickers and wren-tits are claimed to be partial to the fruits of *Toxicodendron* species up to 25% of their diet. Crows have been reported to be fond enough of the fruits to be important disseminators of the species (Burrows, 1895). Poison-ivy fruits in the diet of birds during the winter have been observed by W. R. Overlease in Michigan and Indiana, and by John Verdier for shore birds at Island Beach State Park, New Jersey (both personal communications). Additional relations to wildlife are discussed further under the topic "biological interactions."

Although the lacquer-bearing properties of resins of these plants have been established by Dawson (1956a and b) to be chemically related to those of the lacquer trees of the Orient [*Toxicodendron verniciftuum* (Stokes) Barkley and possibly several other *Toxicodendron* species to a lesser extent], the poisons have never been collected from any member of either section *Toxicodendron* or *Simplicifolia* for commercial use. Only the Pomo Indians of California

ever used the resin for a product: they dyed basket fibers with it (Balls, 1965).

Various American Indian tribes had intriguing uses for poison-ivy and its allies. The Meskwaki, Ojibwe, and Potawatomi used it (presumably *T. rydbergii*) as a poultice on a swelling to make the skin open (Smith, 1928, 1932).

The Ramah Navahoes made an arrow poison from poison-ivy sap mixed with deer's blood and charcoal from a lightning-struck tree, the latter no doubt a connection with black magic (Vestal, 1952). Another version of making this arrow poison added the juices of *Phacelia crenulata* var. *ambigua* Macbr. (Wyman and Harris, 1941). The Navahoes also used poison-ivy *(T. rydbergii)* for good luck in gambling: they chewed a small piece of leaf and gave it to an opponent (Vestal, ibid). The Karok Indians used sticks of *T. diversilobum* to spit salmon steaks while smoking them, and its leaves to cover soaproot (*Chlorogalum pomeridianum* Kunth) when baking it in an earthen oven. The Concow Indians of northern California even mixed the leaves of *T. diversilobum* into their acorn meal when they baked bread. Other northern California tribes simply wrapped their meal in its leaves while baking (Balls, ibid). Some, too, used its supple stems as the warp in weaving baskets (Balls, ibid.).

The Yuki tribe of California used sap from *T. diversilobum* to get rid of warts: they would cut off the wart and apply poison-oak sap to the wound. The same treatment was applied to ringworm and rattlesnake bites (Balls, ibid.). They also used the sap, mixed with mountain hemlock and suet, for tribal markings (John N. Taylor, personal communication). The Yukis also (especially the Tatu or Huchnom branch) used a sprig of poison-oak dipped in water to "keep the women in due subjection." The men, while attempting to conjure up the devil in their meeting-hall, would paint one of their peers, strip him, place a chaplet of leaves over his face to render him incognito, and send him out through the village amid whoops and diabolical

yells. As he cavorted through the village, he would sprinkle wet poison-oak branches in the squaw's faces. Screaming with uncontrollable terror, the women would fall prostrate on the ground. Sworn to silence lest they die while discussing a spook, they would never realize who had, in fact, been their attacker (Powers, 1877).

HISTORICAL ACCOUNT OF THE COMPLEX

The first known reference to poison-ivy in written record dates from the seventh century in China and next from the tenth century in Japan, according to Toyama (1918). Inasmuch as the various species do not grow in Europe, the plants were unknown to Western civilization until explorers visited the New World, seven centuries after the first written record of them in the Orient. Captain John Smith (1609, 1624) is credited with the first reference to the poison-ivy plant in writings on his findings in North America. It was he who originated the common name to the plant since he noted a similarity in its climbing habit of the North American poison-ivy to English ivy (*Hedera helix* L.) or to Boston ivy (*Parthenocissus tricuspidata* Planch.) in the trifoliolate nature of the leaves. He also noted that the plant produces a dermatitis which "causeth itchynge, and lastly, blisters." Probably for reasons of Smith's description, the first published illustration of the plant, and presumably the first reference to it in a work that is even remotely taxonomic, was its appearance in Cornut's "Canadensium Plantarum" (1635) as *Edera trifolia canadensis*, a name which implies a true ivy. (The taxon pictured is most likely not a collection made by John Smith, but a later one from more northern latitudes, and is *Toxicodendron rydbergii*. The details of its pre-Linnaean history, including possible polynomial synonymy, are discussed by Barkley and Barkley (1938).

Toxicodendron is a pre-Linnaean name, not accepted at the generic level by Linnaeus (1753). Tournefort (1700) made the following distinction when he first used the name *Toxicodendron*: that *Rhus* had unequally pinnate leaves and

a villose berry (sic) with a globular nucleus, and that *Toxicodendron* had ternate leaves and a striate berry (sic) with a compressed nucleus. By limiting the genus to ternate-leaved plants, Tournefort would have omitted such close relatives of poison-ivy as poison-sumac and the oriental lacquer trees which persumably he did not know. He also knew neither the African *Rhus* species nor *Metopium*. Moreover, the compressed nature of the "nucleus" (endocarp and its contents?) is highly variable and certainly not a reliable character. In comparing "villose" to "striated" in reference to the fruit, Tournefort contrasted an exocarp character with a mesocarp character. Boerhaave (1727) followed Tournefort in distributing species in the *Rhus* complex in these genera: *Rhus, Toxicodendron,* and *Cotinus,* and he lumped the African species in *Rhus*. Dillenius (1732) likewise preserved *Toxicodendron*. He illustrated poison-ivy and referred to it as *Toxicodendron rectum foliis minoribus glabris*; from the illustration and from a specimen in the Dillenian Herbarium, one can deduce that the taxon which Dillenius had in mind was *T. radicans* subsp. *radicans*. Parkinson (1640), Boerhaave (1727), and Munting (1713) had at one time considered poison-ivy to be a grape (*Vitis*), and Boerhaave (ibid.) referred to its being called an *Apocynum*.

Linnaeus in the Species Plantarum (1753) and Systema Naturae (ed. 10, 1759) recorded 13 species of *Rhus*, although probably none of them was known to him in the field. As Barkley (1963) pointed out, 14 more species had been assigned to *Rhus* by the end of the eighteenth century, including species in *Rhus, Toxicodendron, Cotinus, Metopium,* and the *Thezera* groups. If priority played a role in keeping species in the genera to which they were originally assigned, then *Rhus* was fast becoming one of the more inclusive of angiosperm taxa.

Engler (1881) divided *Rhus* into four sections: *Trichocarpeae, Gerontogeae, Venenatae,* and *Melanocarpae*. DeCandolle earlier (1825) had made the following sections: *Sumac* to be roughly equivalent in Engler's concept to *Tri-*

chocarpeae and *Venenatae*; he also recognized Sect. *Lobadium* to contain some species which Engler later placed in *Trichocarpeae*. The type section *Rhus*, as presently recognized, is equivalent to section *Sumac* DC. = sect. *Trichocarpeae* Engl. Blume (1850) erected the genus *Melanococca* for the black-fruited species of the southwest Pacific region; it corresponds to Engler's section *Melanocarpae*; Barkley (1942) raised this to generic rank as *Duckera*, but did not until 1963 recognize that this name was antedated by *Melanococca*. Brizicky (1963) has changed this to a subgenus of *Rhus*. Section *Thezera* DC. is the earlier name for sect. *Gerontogeae* Engl., which Koch (1853) raised to a subgenus, and Barkley (1942, 1963) renamed as a genus, *Searsia*. For the sake of simplicity, I shall refer to the *Rhus* species of Africa as the *Thezera* group, and those black-fruited Pacific taxa as the *Melanococca* group. A summary, with synonymy and designation of types or lectotypes where needed is given in Brizicky (ibid.) It is further simplified for reference purposes in Table 1. It is beyond the scope of this study to make taxonomic judgments concerning these groups.

Linnaeus described poison-ivy first in the *Hortus Cliffortianus* (1737); he later edited his description of the plant to include the climbing habit and added a description of Eastern poison-oak when he wrote the *Species Plantarum* (1753). The Clifford specimens include one flowering branch of *Toxicodendron rydbergii* and a sterile branch of *T. radicans* subsp. *radicans*. Linnaeus apparently did not recognize poison-ivy to be dioecious, since his symbol for dioecism is missing from the species descriptions.

Eastern poison-oak presents problems that cannot be unraveled any farther back than Linnaeus. Several authors use the same polynomial phrase by which Linnaeus describes the plant known to him as *Rhus Toxicodendron*, but the specimen at the Linnaean Herbarium is apparently the oldest specimen extant, and can be used to verify the Linnaean concept of that species.

It is with Michaux that much of the nomenclatural con-

TABLE 1. COMPARATIVE TREATMENT OF *RHUS*

DeCandolle (1825)	Marchland (1869)	Engler (1881)	Barkley (1937, Emended, 1963)	Brizicky (1963)
Rhus	*Rhus*	*Rhus*	*Rhus*	*Rhus*
sect. *Sumac*	sect. *Sumac*	sect. Trichocarpae, in part		subgenus *Rhus*
sect. *Lobadium*	sect. *Lobadium*	sect. *Trichocarpae*, in part	*Lobadium*	subgenus *Lobadium*
sect. *Sumac*, in part	sect. *Sumac*, in part	sect. *Trichocarpae*, in part sect. *Venenatae*, in part	*Toxicodendron*	subgenus *Toxicodendron*
			Malosma	subgenus *Malosma*
———	———	sect. *Melanocarpae*	*Duckera*	subgenus *Melanococca*
sect. *Sumac*, in part sect. *Thezera*	sect. *Thezera*	sect. *Gerontogeae*	*Searsia*	subgenus *Thezera*

fusion begins. He made *vulgare, microcarpon,* and *quercifolium* varietal names under *Rhus toxicodendron,* whereas *Rhus radicans,* the Linnaean name for poison-ivy, was not used at all. In the several later editions of Miller's *Gardeners' Dictionary, Toxicodendron* and *Rhus* were segregated. In Miller's view, *Rhus* had hermaphrodite flowers and *Toxicodendron* was dioecious. Since both taxa have dioecious members, this character is inappropriate. Miller (1768) discussed ten species of *Toxicodendron,* of which five or six can be referred to the poison-ivy complex. None can be typified by a specimen from the Chelsea Physic Garden, although several can be typified in other ways (see later discussion under the nomenclature of each taxon). A. P. DeCandolle (1825) altered Miller's work by changes in nomenclature, reducing some of his species to varieties, and reverting to *Rhus,* all the while citing Miller as his source.

DeCandolle (1825), Michaux (1803), and later Engler (in DeCandolle, 1883, and in Engler and Prantl, 1897) returned to the use of *Rhus* to the exclusion of *Toxicodendron* as a generic name. It may be significant that in Engler's key to the tribe Rhoideae (1892), *Rhus* is left close to the end where it appears that it might have been a catch-all. Moench (1794) and Rafinesque (1819) recognized *Toxicodendron.*

Engler (1883) aligned the species with essentially the same subdivisions as DeCandolle but, like Michaux, treated all poison-ivies and poison-oaks as varieties of *Rhus toxicodendron,* whereas DeCandolle (1825) made them varieties of *Rhus radicans.* Engler, though attributing his interpretation of this species to an emendation by Torrey and Gray (1838), was nevertheless in error because the Linnaean specimens were extant and would have demonstrated that his several varieties were more closely allied to *Rhus radicans* than to *R. toxicodendron.*

Work in this complex in the nineteenth century began to round out knowledge of distribution. Engler, relying presumably on specimens then at Berlin, had a geograph-

ically very diverse group of specimens at his disposal, for he cites specimens from localities in Japan, Sakhalin, Canada, Mexico, Texas, California, Central and Eastern United States, and Bermuda, making a correct assessment of several controversial specimens, not correctly interpreted since (e.g., *Berlandier* 2035). It is tragic that this array of specimens was destroyed during World War II. The first nomenclatural separation of Asiatic populations was made by Lavallée (1877), and the first for those from Mexico by Sessé and Moçiño (1887).

Otto Kuntze (1891) obliterated the genus *Rhus* as he made wholesale transfers to *Toxicodendron.* His work has little value except that it is the first place that a number of transfers are made from *Rhus* to *Toxicodendron.*

Edward Lee Greene (1905, 1910), as he was wont to do, named 24 new species in this complex, separating related populations on superficial grounds. He even annotated isotypes of his own naming years afterward without recognizing them as the species he had described! He is known to have assigned different names to flowering and fruiting collections from the same population along the Klickitat River in Washington.

Greene, the redoubtable splitter, very sagely pointed out (1905) that for hundreds of years before Tournefort, there was only one *Rhus*, i.e., *R. coriaria*, the coriar's (tanner's) sumac, whose chief use was the source of tannins for the processing of leather. When *R. hirta* (= *R. typhina*) and *R. glabra* were first brought from North America to Europe, Greene continued, there was no question as to the genus of these sumacs. But then poison-ivy appeared on the scene. Presumably the first member of this taxon to reach Europe was *Toxicodendron rydbergii,* the northern representative of the complex. It is unquestionably the first member of the group to be illustrated (as *Edera trifolia canadensis* in Cornut, 1635). This species is likely to have a subterminal inflorescence like the terminal one of traditional *Rhus*, and from the illustrative material that was more commonly available than herbarium specimens in the eighteenth cen-

tury, likely to have been the source of the *Rhus* myth about poison-ivy (even though Greene incorrectly equates Cornut's illustration with *T. vulgare* — *T. radicans* subsp. *radicans*).[3]

One of the Clifford Herbarium specimens, which were the ones which were instrumental in formulating Linnaeus's early ideas about members of this complex, is *Toxicodendron rydbergii*, a non-climbing sub-shrub which superficially has much in common with the habit of *Rhus* species.

In spite of their penchant for splitting, it is significant that E. L. Greene and John K. Small were the first North American botanists who studied the poison-ivy complex carefully, and among the first who knew it first-hand in the field. Gray, Torrey, and Nuttall apparently did not make an intensive study of this group: Britton changed his mind, using *Rhus* in his earlier publications (1894, 1901) and *Toxicodendron* in his later ones (Britton and Shafer, 1908 and Britton and Brown, 1913).

The work of James B. McNair in the early part of this century on the poison-ivy complex is noteworthy for its volume. There has been no more prolific writer on the broad scope of taxonomy, poison chemistry, medical treatment, etc., of the poison-ivy complex. In 1923, his collected works were republished in book form under the title *Rhus Dermatitis*. In 1925, he published a short treatise on the taxonomy of poison-ivy, an inadequate and fairly incorrect assessment of its taxonomy and nomenclature.

In 1937, Fred A. Barkley wrote his doctoral dissertation on *Rhus (sensu lato)* in North and Central America including the West Indies. His treatment of the *Toxicodendron* group was a conservative approach to species and varieties. However, the nomenclatural decisions which he made have been only partially followed subsequently, largely

[3]Greene correctly points out that Miller, in using *T. vulgare*, was using the priority of his day: not that related to *Species Plantarum* (1753), but that of Dillenius (1732), who happened not to use the binomial system.

because he chose the unpopular course of action, i.e., to accept *Toxicodendron* as a genus. He later further split *Rhus* into *Schmaltzia* (1940) (= *Lobadium* according to Brizicky, 1963, and Barkley, 1963), *Duckera* (1957) (= *Melanococca*), and *Searsa* (1957, 1963).

Fernald in his intensive examination of the flora of southeastern Virginia (1950), made further nomenclatural additions to the poison-ivy complex. Although Fernald worked from specimens which he himself had collected in the field, he made some errors of judgment (e.g., naming a new form [*Rhus toxicodendron* f. *elobata*] of Eastern poison-oak based on a character which is confined to female plants), therefore not warranting nomenclatural concern.

A comprehensive summary of the *Rhus* vs. *Toxicodendron* problem, with resolution of numerous dilemmas in nomenclature and typification, was published by Brizicky (1963). Barkley (1963) wrote a rebuttal to this discussion, and so the controversy continues.

CHEMISTRY

From a chemical viewpoint, a study of the active poisons began in 1858 with the work of Khittel who thought he was dealing with a volatile alkaloid. Maisch (1866) and Pfaff (1897) isolated the poisons for study, but it was McNair (1916, 1921) who determined the catechol nature of the poisons, and their possession of unsaturated side chains. Majima and Cho (1908) and Majima (1922) recognized the similarity of poisons in poison-ivy and in the Japanese lacquer tree, calling these substances urushiols after *urushi*, the Japanese name for plants of the *Toxicodendron* group. Majima first synthesized a compound like that of urushiol; Hill *et al.*, (1934) isolated some of the pure poison; and Haack (1940) added to our knowledge of the poison chemistry of related toxic Anacardiaceae from the Dutch East Indies. The exact structure of the side chains and of the number of poisons involved in poison-ivy was determined by Dawson and his students at Columbia University (Symes and Dawson, 1954; Dawson, 1954, 1956).

There are four toxic substances in poison-ivy, all 3-*n* pentadecylcatechol. The four differ only in degree of saturation of the side chain.

GENERIC RELATIONSHIPS OF THE COMPLEX

Toxicodendron is most nearly allied to *Pseudosmodingium*, *Comocladia*, *Metopium*, and the *Rhus* complex, especially *Actinocheita* and *Malosma*. It shares with *Pseudosmodingium*, *Comocladia*, and *Metopium* possession of toxic resins (likely all catechols) and odd-pinnate leaves; in the latter two genera, however, the endocarp is thin and layers of the fruits do not separate upon ripening. Furthermore, the flowers of *Comocladia* are trimerous, whereas those of *Pseudosmodingium*, *Metopium*, and *Toxicodendron* are pentamerous. The drupes of *Pseudosmodingium* share with those of *Toxicodendron* the property of separation of pericarp layers as the fruits mature; however, the drupes of *Pseudosmodingium* possess two, more or less equal, broad lateral wngs. Engler (1881) and Barkley (1957) separated these two genera on the shape of the fruit, with those of *Pseudosmodingium* being reniform and strongly compressed, while those of *Toxicodendron* are subglobose or ovoid and not always strongly compressed. There are several *Toxicodendron* species however, particularly in Asia, (*T. succedaneum*, *T. nodosum*, and *T. verniciflwum*), that have drupes which may be more or less reniform and are strongly compressed, although New World species (plus *T. trichocarpum* of Asia) have subglobose fruits. In fruit and flower morphology, *Toxicodendron* is most closely related to *Rhus* and its allies, *Actinocheita* and *Malosma*, but vegetatively it is more similar to *Metopium* and *Pseudosmodingium*.

The question of whether *Toxicodendron* should be segregated at the generic level from *Rhus* has long been problematical, there being so much force of conviction involved that no series of reasonable arguments in support of either view has much hope of victory. It is necessary at this point to choose a taxonomic path and defend its use in this paper.

It would appear that first the taxon *Toxicodendron* needs to be defined. Secondly, *Rhus* needs to be examined as a composite genus made up of several segregates. Thirdly, the reasons pro and con for segregating these components as genera, i.e., what happens to *Rhus (sensu lato)* in each case, must be evaluated.

McVaugh (1945) made eight recommendations to be followed in segregating genera. Because each of these recommendations will be considered in evaluating the status of *Toxicodendron* and *Rhus*, they are rephrased in summary here:

1. Strong morphological characters or presence-absence of distinctive attributes should be emphasized.
2. There should be no segregation of genera on the basis of characters of minor import unless maintained because of long-held botanical tradition.
3. Not the width of the gap between genera but the taxon's own biological unity should be emphasized. Homogeneity, regardless of degree of overlap of characters with those of other genera, is paramount.
4. One should be guided by diagnostic features of more inclusive genera throughout the complete range of the group, and not by local variations.
5. Decisions in regard to the proposed segregate should not be based upon the equality of relationships between it and some other segregate, but upon the relationships between the segregate and the more inclusive genus.
6. Segregate genera should be sharply delimited. Any species intermediate between the segregate and the more inclusive genus should be relegated to the latter.
7. The security of position of any genus increases rapidly in proportion to the number of differentiating characters.
8. The generic position of a segregate group is strengthened if it has a distinctive geographical range together with more or less distinctive morphological features.

With the exception of item 5, with which I am not in complete agreement, these guides will be discussed and observed.

Toxicodendron as a taxon (without rank specified) may be defined as being made up of plants having the properties of the anacardiaceous tribe Rhoeae which have imparipinnate leaves, poisonous effluvium, dark brown root hairs, exocarp wall cream, yellow, tan, or dun-colored, and white mesocarp that is fatty and waxy with black striations which are in reality peripheral resin canals. The plants have axillary, somewhat loose inflorescences which tend to be pendent under the weight of the ripening fruit when the clusters are large. Pubescence of the fruit, if any, is eglandular. These characteristics have been discussed by Barkley (1937, 1965), Brizicky (1963), and others, but these authors have reached diverse conclusions as to the level of separation of this taxon from any near relatives.

Almost all workers agree that there should be a segregation of *Rhus* and *Toxicodendron*, if only at the section or subgenus level. The question then is: are the characters which segregate these two taxa at least as significant as those which segregate other taxa within traditional *Rhus*, so that justification of the segregation can be made at this time? If not, what arguments may be advanced for retaining the genus *Rhus* in its traditional sense with a group of five or six sections or subgenera?

First, let us look at the status of *Rhus* in the traditional sense. The traits which serve to characterize *Rhus (sensu lato)* are: (1) the tendency of the fruit walls to separate in various ways, (2) nonenlarging calyx in the fruiting stage, (3) presence of one basal ovule, (4) apical position of the stigma and style, (5) staminal number the same as the petals, (6) presence of a functionally one-celled ovary with the hypocotyl against the cotyledons, (7) ovary and fruit not deeply buried within the intrastaminal disc, (8) the ring-porous woods with inter-vascular pitting circular or hexagonal, bordered and alternate, and (9) vessel parenchyma and vessel-ray pitting composed of small, round or

slightly oblong pit-pairs. Most students of the Anacardiaceae agree that *Cotinus*, *Metopium*, and *Actinocheita* should be segregated: *Cotinus* on the basis of simple leaves, long fertile and plumose sterile pedicels, lateral styles, and permanently adhering fruit walls; *Metopium* on the basis of permanently adhering fruit walls, more or less united calyx lobes, marked bands of wood parenchyma, and fairly pulpy mesocarp; *Actinocheita* on the basis of the long silky hairs of the fruit and the presence of a gynophore.

What is left of traditional *Rhus* when the foregoing taxa are removed is a genus which occurs in North America, northern South America, Mediterranean eastern Africa, southern Africa, southeastern Europe through southern Asia to China and Japan, Malaysia, and Polynesia. It possesses red, white, black, yellow, or tan fruits which have either glandular or non-glandular hairs or are glabrous. Its mesocarp is either resinous or waxy. Its resins are either benign or dermatitis-producing catechols. Its flowers are either in dense, terminal thyrses, terminal and lateral compound spikes, or loose lateral paniculate thyrses. Its fruit walls separate upon maturity so that there is adhesion of the exocarp and mesocarp, or of the mesocarp and endocarp. Such divergent characters do not unify *Rhus*.

Once segregated (following the splitting off of *Cotinus*, *Metopium*, and *Actinocheita*), then *Toxicodendron* is a group of plants which shares the presence of poisonous resins, axillary inflorescences, pendent clusters of fruit, tan, cream, or dun-colored exocarps, pollen of less than 32μ in length, plus some additional anatomical characters discussed by Heimsch (1940, 1942) that need further study in some Asiatic species. When the fruits of *Toxicodendron* are pubescent, they are not also glandular. What remains of *Rhus* at this point (including the *Thezera* group, the *Lobadium* group, the *Malosma* group, and the *Melanococca* group) is still heterogeneous for a single genus.

The author admits only a cursory acquaintance with the African *Thezera* group and the South Pacific *Melanococca* group. A new look needs to be made of the *Lobadium* and

Malosma groups; the most recent studies (Barkley, 1937, and Brizicky, 1963) involved only herbarium work. To decide the question of splitting or lumping in the *Rhus* complex, one must examine the complex worldwide, complete with cytological, ecological, and comparative anatomical studies. These investigations are beyond the scope of this paper, yet a decision must be made as to the correct names for the poison-ivy complex to be used herein.

Let us explore the kinds of characters which are used to segregate other genera in the Anacardiaceae (Engler, 1883; Barkley, 1957). *Comocladia* is separated from *Metopium* on the characters of sinuate to spinose leaflets and bony seeds vs. entire leaflets and chartaceous seeds. *Actinocheita* is separated from *Rhus* on the basis of presence of a gynophore and long, silky hairs on the exocarp vs. sessile ovary and hairs on the exocarp being short or absent. *Semecarpus* is separated from *Holigarna* on the basis of a half-inferior ovary and intact petiole vs. an inferior ovary and petiole with one to two lateral splits at the base *Harpephyllum* is distinguished from *Koorderisodendron* on the number of locules in the fruit at maturity (two vs. one). *Gluta* is separated from *Swintonia* because the petals of *Swintonia* enlarge in the fruit, whereas *Gluta* petals are deciduous.[4] *Pseudosmodingium* has reniform, strongly compressed drupes, and pinnate leaves, whereas *Rhus* has subglobose, ovoid, or only slightly flattened drupes and trifoliolate, pinnate, or simple leaves. All these separations of genera within the Anacardiaceae seem to suggest that the number of consistent differences between *Rhus* and *Toxicodendron* is certainly greater than, and of at least the same magnitude as, some of these others. In some other families "good" genera have traditionally been made on the basis of a few characters, e.g., *Canavalia* is segregated from closely related genera of the Phaseoloideae because of its

[4]Current thinking among workers on Flora Malesiana is to unite these two genera into a single genus.

bilabiate calyx (Sauer, 1965), and *Astragalus* from *Oxytropis* on the shape of the tip of the keel petals.

In his revision of the Anacardiaceae, Marchand (1869) poignantly points out: "Personne ne songe, nous le croyons du moins, à rétablir l'indépendance de ces sections pour en faire des genres distincts. Cependant ils sont séparés par les caractères d'une valeur beaucoup plus grande, que ceux qui distinguent encore certains genres de cette famille. Pourquoi cette double maniére d'interpréter la classification? Pourquoi ne pas établir des divisions comparables entre elles? Au moment où le tendance à la division s'accentue à un tel point sur toutes les autres parties de la famille, ici la tendance contraire continue à se manifester. Nous ne comprenons pas pourquoi cette différence existe."

One must be cautious as indicated by Adanson (1757) when he suggested that one cannot choose diagnostic characters of genera when they are incompletely known, because new species might prove to be exceptional. Admittedly, the Far Eastern species of *Rhus* and *Toxicodendron* are incompletely known, but not likely soon to become better known.

The most useful characters for distinguishing *Toxicodendron* from related taxa, in my opinion, are pollen size, presence of poisonous resin in the phloem, exocarp color and pubescence, pendent position of the fruiting inflorescence, and absence of red glandular hairs on pedicels and fruits. There are in addition anatomical differences of lesser importance, but as Barkley says (1963), ". . . an evaluation of the anatomical differences can await more exhaustive studies, and the separation of genera is not dependent on such studies."

The question arises whether the characters which are used to distinguish these genera are consistent in all species. Let us look first at the poisonous nature of the oleoresins.

Literature references to the toxic nature of the various species of *Rhus* are not altogether to be trusted. *Rhus michauxii (Rhus sensu stricto)* of the eastern United States

Coastal Plain and Piedmont has been cited by Sargent (1895) as being highly poisonous, whereas Warren (1909, 1910) correctly disputes this statement. *Rhus trichocarpa* (= *Toxicodendron trichocarpum*) is declared by Rehder and Wilson (1914) to be distinct from *R. vernicifera* (= *T. verniciflauum*) in the "absence of poisonous, varnish-yielding sap." Both of these species have poisonous catechols in abundance. The poisonous nature of *Rhus punjabensis* from India (Chopra, Badhwar, and Ghosh, 1949 and Brizicky, 1963) is still suspect. When I requested of Dr. Chopra a voucher specimen of the *R. punjabensis* which he had in mind when he labeled it toxic, a sample of *R. wallichii* (= *T. wallichii*) was sent. The problem is not uncommon for *Toxicodendron* species of the Far East since they have never been monographed. The best treatment is Rehder and Wilson (1914). Quite recently a seed exchange sent to me from the Soviet Union included a packet labeled "*Rhus silvestris* S. and Z." (= *T. silvestre*) which was in reality *Rhus punjabensis*. It is not enough for an investigator to indicate that a certain species of *Rhus* is toxic; he must verify his determination by a voucher specimen. Otherwise a good case may be made for toxicity among *Rhus* species which are in reality *Toxicodendron* species. Mere reference to the toxicity of *Rhus* in the literature, therefore, need not indicate that they are indeed possessors of the typically poisonous catechols.

The presence of the poisonous sap is easy for susceptible persons to detect in the field, but not so detectable from herbarium specimens. When specimens lack data regarding the toxicity of the plant, one must look elsewhere for suggestion of whether or not the plant was toxic when alive. Inasmuch as the toxic catechols in *Toxicodendron* turn black and generally shiny when allowed to oxidize and polymerize, one may look for evidence of these spots where the leaves and stems have been cut, bruised, or eaten by insects. The tell-tale lacquer-like spots near such wounds may be used to indicate the presence of the toxic substances.

The terminal nature of the *Rhus* inflorescence is open to

some question if the African species are included. In *Rhus* (*sensu stricto* = subgenus *Rhus*) the inflorescence is strictly terminal. Among the lower pedicels, small leaves or leaflike bracts may intrude, but the inflorescence is essentially terminal. The occasional pedicels that have leaf-like structures emerging below them cannot reasonably be considered axillary. The many *Rhus* species in Africa (= subgenus *Thezera*) have distinctly axillary flower clusters, these distinguishing them from the *Rhus* species of North America, southern Europe, and temperate Asia. If the African species are segregated into a separate genus *(Searsia)*, then *Rhus* indeed may be characterized by terminal inflorescences. The *Rhus* species of the western Pacific islands (= subgenus *Melanococca*) has a terminal inflorescence as a rule, but as Brizicky (1963) pointed out, there are exceptions. All inflorescences appear to be thyrses with the terminal flower in each tertiary cluster opening first.

As to fruit color, one must be certain that he is observing a ripe or (in the case of herbarium specimens) a properly dried specimen. Brizicky (1963) has examined many fruiting specimens of *Rhus sensu lato*, and suggests that there is overlap in color between the "brown" fruits of *R. coriaria*, *R. copallina*, *R. javanica*, *R. punjabensis*, and *R. (Toxicodendron) griffithii*. The decidedly brown fruits of *R. coriaria* and *R. javanica* have the character of glandular pubescence linked with the fruit color. The "brown" of the other true *Rhus* species is red or red-brown, except in slowly dried material wherein the color deepens to a dark brown. In the case of *T. griffithii*, the brown is a tan or olive, consistent with the fruit color of *Toxicodendron*.

As will be demonstrated later, the pollen grains of *Toxicodendron* are significantly smaller and often more round (smaller length/width ratio) than those of *Rhus*. Mrs. Kuprianova (1965) has supported the erection of a whole family (Pistaciaceae) as a segregate of the Anacardiaceae, based on pollen grain morphology. It is perhaps not too

extreme to use pollen grain size and shape as yet another set of characters for separating genera.

According to Mr. Joe F. Hennen (personal communication), rusts of the genus *Pileolaria* are genus-specific in the members of the Anacardiaceae which they parasitize. *P. brevipes* and *P. shiraiana* attack only *Toxicodendron* species (*T. radicans* subspp. *orientale* and *hispidum*, *T. silvestre*, *T. succedaneum*, *T. trichocarpum*, and *T. vernicifluum*). *Pileolaria klugskistiana*, on the other hand, finds hosts only in *Rhus hypoleuca*, *R. javanica*, and *R. punjabensis*). Such host specificity seems to support other evidence that these two sumac genera should be recognized as distinct.

The segregation of *Toxicodendron* from *Rhus* appears to be appropriate in view of McVaugh's "laws." There are several strong characters which separate it from all other *Rhus* species, characters which unify the genus throughout its range in both Old and New World. These characters are greater in number and of greater variety than those which separate generally accepted segregates of *Rhus*. One species — admittedly too rare for complete knowledge of it — has the paniculate inflorescence of *Toxicodendron*, yet otherwise possesses *Rhus* characters. It is relegated to the latter as *Rhus paniculata* Wall. Presumably it is not poisonous. There are hybrids and evidences of crossing among species of *Toxicodendron*, but none between *Toxicodendron* and other *Rhus* species, nor even between sections of *Toxicodendron* as herein defined. Their ranges do, however, overlap considerably in Asia and North America. By removing *Toxicodendron* from *Rhus*, each taxon becomes more nearly homogeneous.

TAXONOMIC CONCEPTS

The tendency among taxa in *Toxicodendron* under investigation here is to have allopatric ranges; only two species pairs are sympatric. Among the allopatric taxa, intergrades, representing hybridization or incomplete divergence in the speciation process, occur at the fringes of ranges

where two or more taxa come into contact. Strict genetic isolation does not appear to be operating to the same extent that geographical and ecological barriers do in limiting gene exchange among taxa.

The sections of the genus are recognized chiefly on the basis of vegetative morphology: growth form, phyllotaxy, and nature of the leaves, i.e., simple or compound. The phyllotaxy of section *Toxicodendron* is 3/8, that of section *Venenata* is 5/13, and the leaves of section *Simplicifolia* are whorled. In terms of reproductive morphology, the stamens of section *Venenata* have long filaments and short, globose anthers, but those of sections *Toxicodendron* and *Simplicifolia* have short, subulate filaments and elongate anthers. In the poison-ivy complex, I have recognized as species those populations which are morphologically distinct by more than three characters and which, because of major geographical and ecological barriers to gene exchange, seldom interbreed in the field. Only two sets of species of the complex are sympatric (one barely so), and few interspecific hybrids are known. Fruits have been produced by artificial cross-pollination between *Toxicodendron radicans* and *T. toxicarium*, but *T. toxicarium* possesses a much larger set of unique morphological characters and ecological requirements than does any other species, so that it rarely hybridizes with anything else in nature.

The taxa recognized herein as subspecies of *Toxicodendron radicans* are regarded as geographical segregates with fewer characters distinguishing them from related taxa than were utilized to distinguish species. These subspecies occupy fairly large ranges and seem to intergrade in the area where they come into contact with other subspecies.

The term *subspecies* rather than *variety* is used for the infraspecific units because each of the taxa has a distinctive range, and because there is some variation even within the subspecies. Should a subsequent investigator feel that these variants are worth naming as distinctive taxa, he may assign varietal names as subdivisions of the subspecies. The subspecies group themselves into two distinct categories

according to clusters of characters which they share in common. It was originally my intent to recognize these two groups as subspecies and the individual taxonomic variants as varieties. The group of taxa including *T. radicans* subspp. *radicans*, *orientale*, and *hispidum* would then have been a subspecies divided in range between two hemispheres, whereas other infraspecific taxa with ranges adjacent to subsp. *radicans* in North America have less in common with it and would have been placed in another subspecific cluster.

Because of the relative abundance of these plants and of references to them in both scientific and non-scientific literature, I feel that no good end would be served at this time by adopting a classification with two ranks of infraspecific taxa.

PHYTOGEOGRAPHY AND EVOLUTION

Toxicodendron is primarily a genus of North America and eastern Asia. The range of section *Toxicodendron* (Fig. 26) extends from central China and Japan south to Malaysia and from southern Canada to western Guatemala, Bermuda, and the western Bahamas. The range of section *Simplicifolia* is much more restricted, having been found only in north central Borneo. The range of section *Venenata* (not treated herein) is throughout eastern Asia including Japan and Indonesia with a single species in the United States from southern Quebec to Florida in the eastern third of the country, and a single species in Latin America from Veracruz, Mexico to the highlands of Colombia. The American species of section *Venenata* are *Toxicodendron vernix* (L.) Kuntze and *T. striatum* (Ruiz & Pavon) Kuntze. The former is the well-known poison-sumac which is found in acid bogs and swamps in eastern United States. The latter is an upland tree which occurs in Latin America. The Asiatic members of this section are trees of China, Korea, and Japan, the foothills of the Himalayas, and southeastern Asia. They include the oriental lacquer tree, *T. verniciftuum* (Stokes) Barkley, a tree harvested for the wax in its fruits,

T. succedaneum (L.) Kuntze, and a northern member of the group, *T. trichocarpum* (Miq.) Kuntze, to mention three species. A number of other species are said to occur in China.

It is possible that *Toxicodendron* diverged from *Rhus* in the early Tertiary in China with the rare *Rhus paniculata* Wallich of central China a morphological link between the two genera. This species possesses an inflorescence that is loosely paniculate like *Toxicodendron*, yet terminal like *Rhus*. The color of the fruits on herbarium specimens, which may be misleading, is light brown like *Toxicodendron*. The fruits are also eglandular like those of *Toxicodendron*. The mesocarp is fibrous and barely, if at all, striate, resembling *Rhus*. Due to the paucity of herbarium material in Western Hemisphere herbaria, it has not been possible to test for the presence of catecholic poisons, but lack of lacquer-like spots at breaks in the leaves and lack of similar resin duct striation in the fruit are strongly suggestive of its being benign.

Section *Toxicodendron* with its viney habit appears to be more advanced than section *Venenata*. *Toxicodendron* may well be derived from the common *Rhus* species of Asia, with the multiple leaflet taxa being the older, reduction in leaflets being advanced. On occasion *T. radicans subspp.* produce leaves with more than three leaflets; *T. diversilobum* does so even more commonly. This tendency to produce multifoliolate leaves is interpreted as reversion to an ancestral condition. Section *Simplicifolia* demonstrates reduction to simple whorled leaves, still exemplifying the liana habit, and is interpreted as being highly advanced.

Toxicodendron nodosum may be a link between sections *Toxicodendron* and *Venenata*. This species is scandent, but apparently produces no aerial roots. It will produce leaves composed of as many as seven leaflets, but normally gives rise to only five. In one plant grown in the laboratory leaf primordia initiated during periods of water stress had fewer leaflets than those developing when the plant was abundantly watered. The species appears to combine the multi-

foliolate leaf character and lack of aerial roots of section *Venenata* with the scandent habit and tendency to reduction in leaflet number of section *Toxicodendron*. Because of the importance accorded to habit within the complex, and also the stamen structure, this plant has been placed in section *Toxicodendron*.

Toxicodendron nodosum is found today (Fig. 27) in the Malay Peninsula, Borneo, Java, Sumatra, and Celebes. Backer and Van Den Brink (1965) indicate that Malaya and all the islands of the Sunda Shelf (Java, Sumatra, *et al.*) were a continuous land mass during the Pleistocene and would have permitted a free exchange of disseminules. Presumably *T. nodosum* had a distribution throughout this region during the Pleistocene, its distribution having ebbed and become dissected as the sea rose.

Toxicodendron radicans is a wide-ranging species, having several genetic expressions through North America and eastern Asia. Quoting Asa Gray, J. C. White (1873) notes: "Our *Rhus Toxicodendron*, or poison-ivy, is very exactly repeated in Japan, but found in no other part of the world, although a species much like it abounds in California. Our other poisonous rhus *(Rhus venenata)* is in no way represented in Western America, but has so close an analogue in Japan that the two were taken for the same by Thunberg and Linnaeus, who called them both *Rhus vernix*."

Gray mentions poison-ivy (1846, 1858, 1889) as a typical example of the floristic connection between eastern Asia and North America, especially of the eastern United States. Forbes and Hemsley (1886) felt that the trifoliolate species which Augustine Henry had collected from Ichang on the Yangtze River was "evidently allied to *Rhus toxicodendron* L." Miquel (1867) further recognized the identity of the plant called *Rhus toxicodendron* (*sensu auctt. plur. non* L.) as being in common with Asia and North America. He further hypothesizes a common ancestor. More complete studies of the poison-ivy complex have served only to confirm this affinity. The Atlantic Coast taxon (*T. radicans*

subsp. *radicans*) is more similar in morphology to the taxa of eastern Asia (*T. radicans* subsp. *orientale* and subsp. *hispidum*) than to any other; the three are thus grouped as morphologically closely related subspecies. Considering the present abundance of *T. radicans* in Japan, it is puzzling that the species is not mentioned in any of the older floras of that country (Thunberg, 1784; Siebold and Zuccarini, 1826-70; Blume, 1849-56).

The North American taxon (*Toxicodendron radicans* subsp. *radicans*) which most closely resembles the oriental and fossil ones perhaps represents populations which have been exposed to relatively little environmental change, except glaciation, since their invasion of this region, presumably during Eocene time or shortly thereafter. Populations in other parts of North America have been exposed to mountain-building, glaciation, and changes in climate which have been accompanied by changes in leaf and fruit morphology, possibly of a non-selective nature. A major change has been in the development of dentate, crenate, and lobed leaflet margins. This latter type of margin is most common in populations of *T. diversilobum* a near relative of poison-ivy. It is this form which represents the greatest departure of the leaflet from the primitive, entire-margined form.

Tatewaki (1958) noted that poison-ivy, like certain other Japanese plants such as *Hydrangea petiolaris*, *H. paniculata*, and *Actinidia kolomikta*, has a distribution throughout Japan, the southern Kuriles, southern Sakhalin, and central China. Nakai (1909) had pointed out earlier that it does not occur in nearby Korea, Manchuria, and Far Eastern Soviet Union.[5] Phytogeographically, poison-ivy's oriental distribution may be described as being in the Temperate Eastern Asiatic and Subarctic regions as defined by Engler. It follows Miyabe's line in the Kuriles, being south, but not

[5]Its occurrence in the Soviet Union is restricted to the islands east of the Mainland, over which Russia secured mandate following World War II.

north, of the Etorof Strait (Miyabe, 1890), and is south of Schmidt's line in Sakhalin (Schmidt, 1868, and Tatewaki, 1958). *Toxicodendron radicans* subsp. *orientale* is found (Fig. 36) as far south in the Japanese Archipelago as Yakusima Island, one of the northernmost islands of the Ryukyus (Masamune, 1934). It skips over the more southerly Ryukyus and is replaced in Taiwan by *T. radicans* subsp. *hispidum* (Fig. 38).

In Japan, poison-ivy is common, not in fields, hedges, and fencerows (of which there are few in that country), but in the forests as a denizen of the old forest vegetation. It is not the common intruder into ruderal sites as it is in North America. It has been collected more often in Hokkaido and Honshu than in Kyushu and Shikoku, for the former two islands have been studied more intensively than the latter two.

From regions of more rigorous growing conditions in Hokkaido and the Rishiri Islands, a supposedly non-scandent form has been described as *Rhus rishiriensis*. For lack of any evidence of a genetic difference between this form and the more typical Japanese poison-ivy, they are treated here in synonymy. It is possible that this sub-shrub is an incipient subspecies.

In the central mountains of Taiwan and in the mountains of central and western China, *Toxicodendron radicans* subsp. *hispidum* occurs as a climber or small bush in rocky places. Its distribution in China follows the Yangtze River drainage system of the Hunnan and Kweichow plateaus and foothills of the Tibetan Plateau in Yunnan, Szechuan, Kweichow, Sikang, and Hupeh Provinces.

The Chinese component of *Toxicodendron radicans* is found in two widely disjunct localities, central China and Taiwan. Taiwan is a continental island probably connected to the mainland until Tertiary times, possibly until the Pliocene (Hosokawa, 1954). The Formosa Straits, separating Taiwan from mainland China, are no deeper than 100 fathoms. The natural initial conclusion of the student of the Chinese flora is that the flora of Taiwan would be more

closely related to that of the East Coast provinces south of the Yangtze River, but according to Li (1963) the affinity of Taiwan's mountain flora is with that of central and southwestern China. Even the so-called "endemic" genus of Taiwan, *Taiwania*, has been found in northwestern Yunnan. The phytogeographic link was likely the mountain chain from China and the Tibetan Plateau through the Malay Peninsula to Taiwan, a thoroughfare that has been closed since the Tertiary (Wilson, 1920). According to Hosakawa (1954), Taiwan was connected geologically with continental China during the Pliocene. Hypothetically, the distribution of poison-ivy may have once been continuous from western China to the mountains of Taiwan, and has shrunk in more recent times with interruptions by the sea. Long-distance dispersal cannot be ruled out as the explanation for the disjunct distribution of *T. radicans* subsp. *hispidum*, although no means of transport is suggested at this time.

The mechanism of inter-continental dispersal for *Toxicodendron radicans* is now of some importance. One suggestion to account for the present-day distribution is the shrinking of a once more extensive range with *T. radicans*, or an ancestor, a member of the Arcto-Tertiary flora. One may envision a continuous distribution throughout eastern Asia and North America across a hypothetical connecting land-bridge in the Tertiary when the climate of the boreal lands was probably temperate. This hypothesis would account for the striking similarity between taxa on these two continents — even greater similarity *between* the inter-continental populations of *T. radicans* subsp. *orientale* and *radicans* than *within* the populations of the various taxa in North America. The latter have evolved with the evolution of land forms in North America since the closing of the land-bridge, eastern North America and eastern Asia having remained more stable in the interval than the intervening land mass. No fossils of poison-ivy, however, are known from this intervening mass except that *T. magnifolium* has been found in several Oligocene formations in northern California where *T. radicans* is not found today

(MacGinitie, 1937, and Jack Wolfe, personal communication).

Another possibility for the two-continent distribution of this species is long-distance dispersal, but considering it as part of the Arcto-Tertiary flora is a more logical possibility. The prevailing winds and ocean currents are west-to-east; thus, it is possible that the species may have had its origin in Asia with North America the recipient. However, its closest generic relatives are *Metopium*, *Pseudosmodingium*, and *Rhus* species which are New World in distribution. It seems, therefore, that *Toxicodendron radicans*, like the horse, may have had a North American origin and later migrated to Asia.

In North America, the possible speciation pattern of the past may be analyzed by present-day distributions. There appear to be, in general, only subtle barriers to gene flow. *Toxicondendron radicans* subsp. *radicans* (Fig. 34) is a lowland subspecies, separated from subsp. *negundo* (Fig. 43) to the west by the Allegheny Ridge in Pennsylvania and New York, and the Blue Ridge and adjoining mountains to the south. Zones of overlap and introgression can be demonstrated in the above-mentioned regions (see discussion under Hybrids, Crosses, and Intergrades.) In the north subsp. *radicans* is separated from *T. rydbergii* (Fig. 49) essentially along the 44th parallel of latitude. This phenomenon is especially evident in Nova Scotia where *T. radicans* subsp. *radicans* is found in the southwest portion of the province, and *T. rydbergii* is found farther northeast above the 44th parallel.

Taken together, *Toxicodendron radicans* subsp. *radicans* and subsp. *negundo* occupy much the same range as such genera as *Nyssa* and *Cornus*, which seem to drop out on their western limit where the rainfall is significantly below the 30-inch annual mark (Dressler, 1954). The northern limit of these taxa (and the southern limit of *T. rydbergii*) also correspond. Moreover, subspp. *radicans* and *negundo*, taken together, have a northern limit almost identical with that of *Panicum miliaceum*, *Asparagus officinalis*, *Bromus*

secalinus, and *Arrhenatherum elatius*, as recorded by Hultén (1958-1964) as well as a northern range quite similar to that of a number of others.[6] Presumably when Hultén's work is completed for the dicots, sufficient additional species will be shown to demonstrate a similar distribution to suggest a phytogeographic line at this location in Canada and upper United States.

In further support of the existence of a phytogeographic tension zone here, one might note the southern limit of *Toxicodendron rydbergii*. It is identical with that of *Myrica gale*, *Oxalis acetosella*, and *Goodyera repens*, all of which, like *T. rydbergii*, have an extension of their ranges along summits of the central Appalachians south to Virginia. *Equisetum palustre* has the same southern limit as *T. rydbergii*, and in addition demonstrates a southward continuation along the shore of Lake Michigan as does *T. rydbergii*. Other taxa show a similar, although not identical, southern limit [7] (Hultén, 1958, 1964).

This tension zone as expressed in Michigan has been the subject of several studies involving pollen, plants, animals, and Indian tribes. Potzger (1948) pointed out that climatic factors are less varying over most large geographical distances than they are within the small latitudinal distance of about sixty miles under consideration here. *Quercus* declines in forests north of the zone, whereas *Pinus* does so south of it. Livingston, too (1903, 1905), noted Kent County as the northern limit of many typically southern plants and the southern boundary of the pine forest region. Livingston tends to believe soil factors are controlling in the distribution whereas Potzger (ibid.) feels that the "mas-

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[6]*Bromus japonicus*, *Setaria viridis*, *Poa compressa*, *Holcus lanatus*, *Athyrium filix-femina*, *Phragmitis communis (sensu lato)*, *Osmunda cinnamomea* var. *cinnamomea*, *O. claytoniana*, var. *claytoniana*, *Alisma plantago-aquatica*, *Potamogeton nodosus*, *Cyperus flavescens*, *Ruppia maritima*, *Typha latifolia*, and *Carex atherodes*.

[7]*Carex flava*, *Subularia aquatica*, *Asplenium viride*, *Equisteum pratense*, *Carex vaginata*, *C. disperma*, *Calypso bulbosa*, *Eriophorum alpinum*, *Dryopteris fragrans*.

ter control" is climate. "There is every evidence that the forest tension zone is climatically transitional, where a number of climatic factors, especially extremes, are closely spaced latitudinally, and the forest is merely expressing the biological values of these environmental factors."

He cites these dividing lines at the tension zone: average depth of forty inches of frost penetration, the divide of average date of daily normal temperatures above 50°F between 1 April (to the south) and 1 May (to the north), a similar divide of the beginning of daily normal temperatures above 68°F ("beginning of summer") between 15 June (to the south) and 1 July (to the north), boundary of the number of days with temperature constantly below freezing in the shade between 30 and 60, and a difference of a month and a half in length of continuous snow cover.

Cleland (1966) has noted this tension zone as the boundary between the hunter-gatherer livelihood of Indian tribes and the agricultural one. Furthermore, north of the line, no mastodon fossils nor arrowheads have been found. Van Faasen (unpublished) has mapped chromosome patterns in species of *Aster,* showing that within one section of the genus (section *Aster*) with $n = 5$, almost all members occur in the tension zone or south of it: and all species where $n = 9$ (except *A. ciliolatus*) occur in the southern two-thirds of the Lower Peninsula of Michigan, essentially in the tension zone and south of it.

This ecotone extends across the southern lobe of Ontario, upper New York State, and New England at approximately the 44th parallel of latitude. It is possible that the same factors discussed above have contributed to the distribution patterns of poison-ivy taxa, collectively becoming the barriers to gene flow and factors enhancing speciation. Krause and Kent (1944) discuss this zone in New England. The range of *Toxicodendron rydbergii* is in western United States and Canada under similarly rigorous environmental conditions, especially that of reduced rainfall. It occurs west of a tension zone that runs northeastward through western Texas and Oklahoma, central Kansas, and the

southeastern portions of Nebraska, Iowa, and Wisconsin, influenced chiefly by the rainfall which is less than 30 inches west of the zone. Curtis (1959) identifies this tension zone as the boundary between the prairie-forest margin and the northern hardwoods province, noting plant, bird, and fish species which have the edge of their ranges there.

Two of the taxa which occur in Mexico have ranges which follow the major mountain ranges of that country. *Toxicodendron radicans* subsp. *barkleyi* (Fig. 41) is found in the Sierra Madre Oriental, extending south to the Sierra de los Cuchumatanes in western Guatemala and the Isthmus of Tehuantepec. Subsp. *divaricatum*, on the other hand, follows the Sierra Madre Occidental (Fig. 41), although its northern limit continues into the mountains of southeastern Arizona. The two subspecies intergrade in the trans-Mexican volcanic belt, especially in Jalisco and Michoacán.

The taxon which is closest morphologically to *Toxicodendron radicans* subsp. *barkleyi* is subsp. *pubens* (Fig. 39) of the southern Mississippi drainage in the United States. Both forms have pubescent leaves, differing only in that subsp. *pubens* has pronounced notches on the leaflets and broad leaflet bases, whereas subsp. *barkleyi* lacks these features. Non-productive branches of subsp. *barkleyi* revert to a lobed form, although maintaining a narrower leaflet base than does subsp. *pubens*. There have been studies which have noted a phytogeographical connection between plants of the southeastern United States and Mexico (McVaugh, 1943, Crum, 1951, Martin and Harrell, 1957 and Sharp, 1966), especially from the Ozarkian area where subsp. *pubens* is indigenous. I postulate that the ancestors of this pair of taxa (subsp. *barkleyi* and *pubens*) once existed from the south-central United States continuously down the mountain chain of the eastern branch of the Mexican Cordillera. As Dressler (1954) has suggested for disjuncts between Guatemala and the Ozarks, these plants became separated into two distinct populations because of decreased rainfall in Texas and northeastern Mexico in early Pleistocene. The northern portion has expanded its range into

the Lower Mississippi Valley into the former Eocene embayment region, and portions have, in modern times, formed hybrids with taxa in adjacent regions over a large area. The southern population has also expanded its range down from the mountains into various provinces of eastern Mexico.

Highly variable populations of subsp. *barkleyi* in northern Mexico posed problems of interpretation until late in this investigation. They show some variation in degree of leaf pubescence, but more significantly, tend to have leaflets which are broad at the base and more deeply notched on the leaflet margins, both departures from less variable populations to the south. Of these, one population is represented by a large number of herbarium specimens collected by Palmer near Ciudad Victoria (Tamaulipas) in 1907; another I have examined myself on two visits to a site near Galeana (southern Nuevo Léon). These populations are now interpreted as evidences of the common ancestry with subsp. *pubens* to the north, a taxon which has broader leaflets and notched or nearly lobed leaflet margins. Farther to the south in the range of subsp. *barkleyi*, there is greater uniformity in the entire nature of the leaflet margin, dense leaflet pubescence, and elliptical nature of the leaflet margin.

There appears to be a similar tie between the population of poison-ivy from the Edwards Plateau region of Texas (*Toxicodendron radicans* subsp. *verrucosum*, Fig. 39) and the taxon of the western part of Mexico (subsp. *divaricatum*, Fig. 41). Both have completely glabrous leaves and shoots except for an occasional population with small tufts of hairs in major vein axils on the lower leaflet surface, a character which possibly hearkens back to a more distant ancestral type, the Asiatic, Atlantic and Gulf Coast cluster of subspecies. I therefore postulate that there was an original connection in the range of the ancestors of subsp. *verrucosum* and *divaricatum* through the late Tertiary in the province of parallel ridges in northern Mexico, that the population was separated into two phases during Pleisto-

cene submergence of northern Mexico, and southern Arizona (see Eardley, 1962), and that the two populations have evolved *in situ* ever since. The northern Edwards Plateau population has become distinctive by the prominent sharp lobes on the leaflets; the southern (Mexican) population demonstrates narrower, entire leaflets. The southern expression, subsp. *divaricatum*, has in recent times expanded its range along the Mexican Highland into southeastern Arizona; the northern expression, subsp. *verrucosum*, has begun to extend from the limestone of the Edwards Plateau and Arbuckle Mountains into adjoining country to the south and east.

Western poison-oak, *Toxicodendron diversilobum* (Fig. 31), is a likely descendant of the ancestral *T. magnifolium*, or other early form which is known from Western United States. The fossil record shows divergence from other North American taxa at least as far back as the Pleistocene in the western part of the country. Fossil seeds of *T. diversilobum* of Pleistocene age have been found in various parts of California (Potbury, 1932, and Mason, 1934).

Today, all of the North American taxa are denizens of altitudes below 1220 m (or to 1830 m in the Southwest) and are not able to cross high mountain barriers, notably the Cascades. Such populations, which grow west of the Cascade Mountains, the Great Basin, the Sierras, and the Mojave Desert, have been isolated from their eastern counterparts long enough — starting in Miocene time — to have undergone the modification necessary to be recognized as a distinct taxon, based largely on leaf and fruit morphology. The uplift of the Cascades was late Pliocene and early Pleistocene (Williams, 1957); the block faulting of the Great Basin was late Tertiary and Pleistocene (Kay and Colbert, 1965); and the greatest tectonic activity in the Sierras was in the late Miocene (Kay and Cobert, *ibid.*). These landforms thus formed separate *T. diversilobum* and *T. rydbergii* today. Only where the Columbia River cuts through the Pliocene basalts of the Cascade Mountains have Western poison-oak and poison-ivy mingled and inter-

bred. The hybrid progeny show introgressive variation in leaf shape and fruit pubescence ranging from the western to the eastern taxa. (See discussion under "Hybrids, Crosses, and Intergrades.")

The origin of *Toxicodendron toxicarium* (Fig. 51) is open to question. Although the remote ancestry and derivation of this plant remain obscure, its recent history probably can be synthesized from what is known or postulated of other sandhills species. This plant inhabits chiefly the fall-line sandhills of the Carolinas and adjoining states, but also has moved into pine barrens, has reached up the Mississippi Valley to southern Missouri, west to Texas, and north to New Jersey. It has passed freely into the xeric soils of the Piedmont and lower mountains. Duke (1961) describes plants such as these as being indigenous to the sandhills, but not endemic there; rather, they are able to become established in ecologically similar habitats.

The sandhills and pine barrens floras seem to be determined by the inability of roots to grow rapidly enough to penetrate the sterile upper soil horizons to reach the richer soils below (Wells and Shunk, 1931) and to utilize nutrients in the surface decomposition zone. *Toxicodendron toxicarium* is such an example; its roots rarely reach the horizon of illuviation. Plants which comprise these floras were probably the first to colonize the available sandy habitats uplifted after the Cretaceous inundation (Duke, 1961). Where were they before this?

Fernald (1937) postulated a Virginia-centered classification of floral elements that were later distributed throughout the sandhills area of the fall-line. Duke (ibid.) feels that a northern Florida center is more meaningful. For those who believe in the "Orange Island" refugium during the Cretaceous (Woodson, 1947; Vaughan, 1910; Cooke, 1945; Goin, 1958), such a northern Florida center seems most reasonable.

Following late Tertiary uplift, there might have been a dichotomous radiation of migration: northward along the xeric sands of the Cretaceous Tuscaloosa formation to the

middle Atlantic states and west through the xeric sands across the Gulf Coastal Plain. The flora which developed in the sandhills may have evolved along with the development of the sandhills as a geomorphological formation since the late Tertiary.

Toxicodendron toxicarium might well have been one such species. There are a number of examples of plants which share this dichotomous distribution (Duke, 1961, and Gould, 1962): *Pinus taeda, Prunus angustifolia, Centrosema virginianum, Desmodium strictum, Lespedeza striata, Polygala polygama, Croton glandulosus, Leiophyllum buxifolium, Breweria pickeringii, Ruellia carolinensis, Elaphantopus carolinianum, Eupatorium rotundifolium, Heterotheca subaxillaris, Danthonia sericea, Aristida lanosa, Gymnopogon ambiguus, Panicum aciculare, P. trifolium, Sacciolepis striata, Andropogon ternarius, A. elliottii, Cyperus retrofractus, Carex complanata, Scleria nitida, Smilax glauca,* and *Toxicodendron toxicarium.* As Harper (1906) has noted, those plants whose ranges cross the fall-line (as does *Toxicodendron toxicarium*) nearly all occur in the pine barrens as well as in the sandhills.

If *Toxicodendron radicans* were an ancestor of *Toxicodendron toxicarium,* then *T. toxicarium* was gradually modified for characters of selective advantage in the xeric habitats in which it grew, i.e., pubescent leaves, reduced habit, revolute leaflet margins — all considered at one time or another as water-saving devices. Its ancestry to poison-ivy may be seen in its trifoliolate condition and pubescent fruits, which is a primitive character in the *T. radicans* group.

Part of the clue to the relations of *Toxicodendron toxicarium* might be found in *T. radicans* subsp. *eximium.* Both have narrow ecological requirements. *Toxicodendron toxicarium* inhabits scrub oak forests (often with pine) that are quasi-savannas. The regions are open, seldom with trees more than a foot in diameter, often subject to burning. The soil is generally sand of low nutrient content. The range of *T. toxicarium* is typically the Gulf and Atlantic Coastal Plains, but has extended into adjacent regions

where a sandhills vegetation prevails. *Toxicodendron radicans* subsp. *eximium* (Fig. 41) occurs in mesic canyons in southwestern Texas and northern Mexico, but has the distinction of being the rarest of the taxa here considered.

The affinities of these taxa are obscure. Both have pubescent leaves; both have predominantly lobed leaflets; both have fruits which are pubescent to a greater or lesser degree. Several floras have mistakenly included subsp. *eximium* in *Toxicodendron toxicarium.* These taxa are more like each other than they are like anything else, and have no close affinities with other taxa in the complex. Their chief difference is habit and degree of leaflet lobation. Subsp. *eximium* is completely separated from any taxa in adjoining areas and hence demonstrates no intergrading or hybridization that is known. *Toxicodendron toxicarium,* on the other hand, can form hybrids with *T. radicans* subsp. *radicans,* although such hybrids are rare in nature. It is possible that *T. toxicarium* shared a common ancestor with the poison-ivies because they behave as not distant relatives in their ability to cross, yet their actual relation remains obscure. Perhaps *T. toxicarium* and *T. radicans* subsp. *eximium* are more closely related to each other than either is to other taxa — they do share many morphological similarities — but their present ranges seem difficult to reconcile on the basis of anything but chance long-distance dispersal.

Since the modern distributions of the poison-ivies must be related to Pleistocene glaciation, we must attempt to reconstruct their postglacial history and attempt to account for where the various taxa must have been during the Pleistocene. There is some evidence from present distribution patterns that several of the taxa in question may have resulted from separation by the glaciers of fewer once-widespread ancestral forms into separate populations. At the height of glaciation, subsp. *radicans* was undoubtedly restricted to a region of southern and eastern United States south of the ice sheet. At the same time, subsp. *negundo* might have existed in a refugium in the sand plains of the

central states or in the Ozark region; it may have evolved from subsp. *radicans* during the separation by ice sheet and mountains (Appalachians) at this time. Subspecies *pubens* probably occupied essentially the same pattern as today in the lower Mississippi Valley.

With release from the ice, the *terra nova* was free to be invaded by disseminules of plants such as *Toxicodendron radicans* behind the influx of spruce, fir, willow, and aspen. The northern taxon, *T. rydbergii*, probably invaded from the west through a northern route, coming to occupy land north of the 44th parallel of latitude across eastern United States and Canada. Subspecies *radicans* migrated northward along the Atlantic Coast and lower slopes of the Appalachians while subsp. *negundo* invaded along a northeasterly path through the center of the country into western New York and Pennsylvania. In relatively recent times, *T. rydbergii* may have expanded its range southward along summits of the Alleghenies and the Blue Ridge by long-distance dispersal or inadvertent introduction; several of the southerly outlying populations in mountain areas are associated with road gravels and recent construction. These patterns of post-Pleistocene invasion follow suggestions of migration of many other plants described, for example, by Braun (1950), Fassett (1941), and Iltis (1965, 1966, and personal communication).

In the present Ozarkian region, the systematics of poison-ivy becomes very confusing. The region of southern Missouri, eastern Oklahoma, northwestern Louisiana and most of Arkansas (with the exception of the "Delta" region of cotton-growing country along the Mississippi River) present problems of poison-ivy identity. In this area, which is complex lithologically and pedologically, there appears to be extensive variation over a large area, presumably the result of large-scale introgression among several subspecific taxa. Populations may show a complex of the leaf pubescence of *Toxicodendron radicans* subsp. *pubens*, the entire leaflet margin character of subsp. *radicans* or the lobing on the leaflets of subsp. *negundo* or *pubens*, tufts of hairs

in the vein axils of the lower leaflet surface as in subsp. *radicans* or absence of such hairs as in subsp. *negundo* or *pubens*, the glabrous fruit surfaces of subsp. *negundo* or *pubens*, or the pubescent fruits of subsp. *radicans*, etc. This region has had varieties of poison-ivy indigenous for a longer time than any of the glaciated country, so that there has been a longer time for migration, introgression, and exchange of genes. There appear to be no barriers to gene exchange among the subspecies, neither of the physical environment nor of biological mechanics. The activities of man in altering the landscape will probably enhance this process of gene exchange in the future. No conclusions other than the probability of hybridization between the two subspecies seem to be warranted until experimental studies and additional field work are carried out in this area.

In summary, one might suggest the following as the pattern of development and evolution of the poison-ivy complex in North America. The ancestral form is that which occupies the Atlantic and Gulf Coastal Plain (*Toxicodendron radicans* subsp. *radicans*). The combined forces of the early Cenozoic uplift of the Alleghenies and Pleistocene glacial ice separated this population into two facies which have produced subsp. *negundo* to the west and maintained subsp. *radicans* in the east. The Ozarkian and Mexican populations were continuous until the deserts of the early Pleistocene were formed. Likewise, a western counterpart in subspp. *verrucosum* and *divaricatum* exists with separation in the Pliocene or late Miocene due to faulting and uplift in the American Southwest. The far western populations have been separated into distinct populations since the uplift of the Sierras and Cascades and the block faulting of the Great Basin. In regions of more rigorous growing conditions, the evolution of *T. rydbergii* may have progressed at a more rapid rate so that this taxon possesses more distinctive characters than the others in the complex. The spread of *T. toxicarium* is, no doubt, late Tertiary in age.

One more case of poison-ivy distribution bears mention-

ing. In the late 1950's, a case of poison-ivy dermatitis showed up in the Union of South Africa near Cape Town. This was anomalous since there was no known poison-ivy on the African continent. It was traced to a specimen of *T. radicans* which was climbing the side of a house in that area, introduced at some time since 1950 (Ross, 1959). The plant has since been removed from South Africa.

CONSTANCY OF CHARACTERS

The constancy and dependability of characters expressed in the poison-ivy complex has relevance to the determination of which characters should be used for taxonomic purposes. One reason for the confusion among taxonomists in the past regarding the number of taxa in the complex has been the profusion of characters which have been used for classificatory purposes. Determination of character constancy has been based herein on uniformity within a region, especially when a character is found (or is absent) in various specimens from a mass collection of a single clone.

Almost all workers have considered the fruits to be of special significance, chiefly in regard to presence or absence of fruit pubescence. Anatomical studies reveal that the trichomes on the fruits are hollow, septate hairs that have been produced by evaginations of the exocarp wall. Small papillae are considered to be incipient or reduced hairs; therefore either trichomes or papillae on the fruit walls are considered an expression of the same character, varying only in degree. Fruits of *Toxicodendron radicans* subsp. *orientale*, for instance, are always either pubescent or papillose, never glabrous.

Fruit pubescence is considered to be primitive in this complex, its greatest expression being found in the populations of China. It may appear secondarily in a few populations in advanced forms which typically have lost their pubescence through evolution, i.e., populations from parts of Indiana and Oklahoma in *Toxicodendron radicans* subsp. *negundo*. It may also become reduced or lost entirely in a

taxon wherein it has been an important character. There appears, for example, to be a cline within this character's expression in *T. radicans* subsp. *radicans*, a taxon normally distinguished by its pubescent fruits. From central Georgia to southern Florida, the fruit hairs appear less and less pronounced and more sparse, until populations from Key West, Florida, are decidedly glabrous. The character of fruit pubescence is still considered of importance within the *T. radicans* group because it helps unify most populations of this taxon. When it does vanish from the population, it does so over a fairly gradual cline. Except for extreme southern Florida populations, then, fruits are pubescent in this subspecies, even though occasionally only sparsely so. Pubescent or papillose fruits are found in all fruiting populations of *T. diversilobum* and *T. toxicarium*.

The fruits of the genus *Toxicodendron* are typically laterally flattened. Only in eastern North American taxa are they globose or subglobose. *Toxicodendron striatum* of Central and South America and *T. diversilobum* show a tendency to flattening, but the other taxa of North America have globose or subglobose fruits. This character then is dependable within species groups.

Habit of the plant and presence or absence of aerial roots are dependable characters. *Toxicodendron toxicarium* and *T. rydbergii* and supposedly *T. nodosum* never produce aerial roots in the wild, the former two being sub-shrubs.

A single leaf does not a taxon make! Although most keys to poison-ivy taxa have been based on fruit characters, more new species have been described on nuances of leaflet morphology than on any other single trait. Many such taxa have been described on the basis of only one or two specimens. Most of these are undependable characters because they vary within as well as among populations.

Number of leaflets is fairly standardized at three in *Toxicodendron radicans*, *T. diversilobum* and *T. toxicarium*. However, a number of populations are known in which additional leaflets are produced year after year (Gillis,

1960). In *T. diversilobum* it is common for a clone to produce a few leaves consisting of five leaflets. As many as eleven leaflets have been found. In subspecies of *T. radicans* the production of multiple leaflets is more sporadic, in *T. toxicarium*, rare. Although multiple-leaflet forms exist, they do not deserve taxonomic recognition. *Toxicodendron nodosum* characteristically has more than three leaflets.

Juvenile leaves are atypical as are shade leaves, and particularly leaves from procumbent stems. Leaves used for diagnostic purposes should always, in erect and liana forms, be chosen from the climbing stems or terminal branches. There is too much variation in shade leaves, those from creeping branches and those buried within the center of a large shrub, for these to be of diagnostic value.

If mature leaves on mature flowering or fruiting branches are selected for diagnostic purposes, then the characters of importance and dependability are: length-to-width ratio, presence or absence of tufts of hairs in axils of vein branches from the midrib on the lower surface of the leaflets, nature of the leaflet apex and base (especially on the terminal leaflet), nature of the leaflet margin (especially on the terminal leaflet), pubescence of the lower surface of the leaflet, and presence or absence of pubescence on the petiole. The length of the petiole and prominence of veins on the leaves are critical in a very few taxa. If a choice of leaves is possible, one should select them from both male and female material, for they often differ in lobation and serration between the sexes in the same population. Young, emergent leaves do not often have all diagnostic characters expressed well enough for accurate determination.

Leaf thickness is of little reliability in determining taxa, since this character is highly variable, often related to the thickness of the cuticle and not to layers of mesophyll tissue. Leaf size is more often than not related to light environment, larger forms being sun (sic) leaves. Notching and serration are good only within certain broad limits. Upper leaflet pubescence is not constant within taxa.

POLLEN MORPHOLOGY

Pollen was examined from species of *Rhus, Toxicodendron, Metopium, Actinocheita,* and *Schinus* to determine the significance of pollen morphology on the classification of *Toxicodendron* and related taxa.

The study was an attempt to determine the degree of variation among genera, species, and subspecies of the tribe Rhoeae, as well as to evaluate pollen characters as a means for distinguishing the taxa.

For most species studied, anthers were removed from materials in the Michigan State University Herbarium (MSC), chiefly from my own collections. Two samples were taken from specimens at other herbaria. Pollen was obtained from the type species of the genus *Rhus* (the south European and western Asiatic *R. coriaria* L.), from the two poison-oak species, from three American species of *Rhus sensu stricto,* and several taxa of poison-ivy from North America and Japan. Two species of *Toxicodendron* sect. *Venenata* and the one of sect. *Simplicifolia* also were examined. One sample each was taken from *Metopium, Actinocheita,* and *Schinus.* The source of the materials used in this study is given in Table 2.

Dried anthers were collected from herbarium specimens and stored in vials of glacial acetic acid. Acetolysis was achieved in the following manner. Pollen and anther material was centrifuged at 1000 rpm; the acetic acid was decanted. Acetic anhydride was added to the mixture and the whole mixture centrifuged. The supernatant liquid was decanted and 5 cc of freshly prepared acetolysis mixture was added (one part conc. H_2SO_4 and nine parts acetic anhydride). The acetolysis mixture was heated quickly over a Bunsen burner to boiling. It was then centrifuged immediately and decanted as close to the residue as possible in order to remove most of the acetolysis mixture. Seven to 10 cc of water were added to reduce the specific gravity of the remaining liquid and to wash the grains.

The washed mixture was centrifuged and decanted. Ten

TABLE 2. SPECIMENS USED FOR POLLEN STUDIES

(MSC Herbarium unless another herbarium is indicated by abbreviation in parentheses)

Species	Locality	Collector and Number
Rhus coriaria	U.S.S.R.	——
R. glabra	Oklahoma	*DeBarr* 349
R. typhina	Ingham Co., Mich.	*Gillis* 2904
R. copallina var. *copallina*	Sapelo Island, Ga.	*Gillis* 3969
R. copallina var. *leucantha*	Alachua Co., Fla.	*Gillis* 3936
R. punjabensis var. *sinica*	Leang Wong Mt., Yunnan, China	*McClaren* U-614
Toxicodendron diversilobum	San Mateo Co., Calif.	*Mason, s.n.*
T. toxicarium	Alachua Co., Fla.	*Gillis* 4315
T. toxicarium	Richland Co., S.C.	*Gillis* 4558
T. radicans subsp. *radicans*	Dade Co., Fla.	*Craighead, s.n.*
T. radicans subsp. *radicans*	Richland Co., S.C.	*Gillis* 4569
T. radicans subsp. *orientale*	Noboribetsu, Japan	*Gillis* 4743
T. radicans subsp. *negundo*	Ingham Co., Mich.	*Gillis* 2464
T. rydbergii	Delta Co., Mich.	*Gillis* 3645
T. vernix	Ingham Co., Mich.	*Gillis* 3598
T. trichocarpum	Noboribetsu, Japan	*Gillis* 4724
T. nodosum	Larut, Perak, Malaya	*King* 5637 CAL)
T. griffithii	N. Lakhimpur, Assam	*Panigrahi* 27703
T. borneense	Mt. Kinabalu, Sabah, Malaysia (type)	*Haviland* 1198 (K)
Metopium toxiferum	Dade Co., Fla.	*Gillis* 4398
Actinocheita filicina	Tehuacan, Puebla, Mexico	*Gillis* 3720
Schinus molle	Cuapiaxtla, Puebla, Mexico	*Gillis* 3714

cc of water were added, the mixture shaken, and the foam broken up with a few drops of methanol. The mixture was again centrifuged, the supernatant liquid decanted, and the residue was suspended indefinitely in glycerin-water mixture (1:1). The pollen was again shaken and centrifuged and then a saturated solution of safranin in ethanol was added for 30 seconds, and the mixture centrifuged. One washing with ethanol, followed by centrifugation, was carried out. A small amount of glycerin jelly (enough to cover the residue) was added and heated to melt (but not boil). By means of a pipette, a portion of the mixture was transferred to each of several clean coverslips. The material was smeared evenly with a toothpick and allowed to dry. The coverslip, when dry, was affixed firmly to a slide by Canada balsam. Ikuse (1956) prefers not to use balsam because he claims the shape of the pollen grain changes as the balsam dries. Inasmuch as all my slides were prepared in the same manner, any change would probably affect all of them more or less uniformly.

Photographs were made under the following conditions: Zeiss research microscope and Exacta camera, full-length tube, optovar at 1.60, iris diaphragm at 4, oil immersion objective (100X), 8X ocular, green and neutral density filters. Because of vibrations due to movement of the shutter, time exposures were employed. Photographs were made with Kodak Plus-X film.

Measurements of acetylated pollen grains were made at a magnification of 1280 X with a calibrated ocular micrometer in the microscope. A total of 15 grains was measured for each "population," three grains on each of five slides. Sets of microscope slides of acetylated grains have been filed in the Herbarium and in the Palynological Laboratory of Michigan State University.

All pollen grains of Anacardiaceae studied are tricolporate (tritreme),[8] finely reticulate (striate-rugulate) with

[8]Terminology follows Faegri and Iversen (1950), Selling (1952), Erdtman (1952), Erdtman and Vishnu-Mittre (1958), Erdtman and Straka (1961), and Kremp (1965).

Table 3. Summary of pollen measurements — selected Anacardiaceae measurements are in microns, 15 grains per set

	Length		Width		Mean Length-width Ratio
	Range	Mean	Range	Mean	
Rhus coriaria	31.5 - 40.8	34.89	27.5 - 33.1	29.03	1.20
R. glabra	36.5 - 45.6	40.67	25.9 - 35.9	32.45	1.25
R. typhina	38.0 - 43.2	39.70	32.6 - 40.0	34.95	1.14
R. copallina var. *copallina*	35.1 - 48.0	39.99	27.0 - 39.2	30.93	1.29
R. copallina var. *leucantha*	37.0 - 45.5	40.31	28.5 - 34.0	31.22	1.29
R. punjabensis var. *sinica*	30.8 - 34.4	34.43	21.4 - 25.7	25.24	1.36
Toxicodendron diversilobum	25.0 - 29.5	28.14	21.0 - 27.4	24.41	1.16
T. toxicarium (Fla.)	22.5 - 27.8	25.30	18.5 - 26.6	21.53	1.18
T. toxicarium (S.C.)	23.5 - 26.0	25.15	19.5 - 23.8	21.16	1.21
T. radicans subsp. *radicans* (Fla.)	23.0 - 28.0	25.95	20.0 - 23.1	21.22	1.22
T. radicans subsp. *radicans* (S.C.)	22.6 - 28.5	25.08	18.9 - 26.6	20.97	1.20
T. radicans subsp. *orientale*	21.0 - 30.0	27.77	20.0 - 23.5	21.97	1.26
T. radicans subsp. *negundo*	23.0 - 28.5	26.11	19.0 - 25.0	21.75	1.20
T. rydbergii	25.0 - 32.0	27.59	22.5 - 30.0	24.41	1.13
T. vernix	25.7 - 29.0	27.14	25.4 - 27.5	26.16	1.04
T. trichocarpum	25.6 - 32.5	27.95	22.5 - 27.0	26.16	1.13
T. nodosum	20.8 - 28.5	26.38	17.6 - 22.1	19.09	1.31
T. griffithii	21.1 - 24.4	23.38	18.8 - 21.4	20.33	1.15
T. borneense	25.6 - 30.4	27.84	25.6 - 29.6	27.28	1.02
Metopium toxiferum	24.9 - 28.2	25.75	18.4 - 25.1	22.48	1.15
Actinocheita filicina	25.1 - 34.0	28.15	23.2 - 27.6	26.15	1.08
Schinus molle	22.5 - 25.5	24.15	21.0 - 26.1	24.25	1.00

long, tapering, sharply defined transverse furrows (sulci). The furrows become approximate, but do not meet, at the poles which are slightly apiculate. In each colpus, there is a large, oblong germ pore, wider than the furrow, whose equatorial diameter equals at least two meridional diameters, each possessing a porous vestibulum with centripetally developed lips. The colpi are zonicolporate, i.e., arranged parallel to the polar axis. The ektexine is slightly raised above the general surface at the pores; the endexine is also thickened internally at the edge of the colpus, forming a ridge or rib (distinct costae transversales). The nexine is incrassate toward the apertures. The exine is heavy, finely reticulate, pitted, or occasionally granular with pits tending to occur in rows. The reticulum is small-meshed with irregular and varied anastomoses bearing columellae conjunctae in the ornamentation. The tegillum is thick; its edge in cross section is slightly wavy or smooth. The exine at the edge of the pores thickens from 1.5μ of the mesocolpium to about 3.0-3.5μ. Heimsch (1940) describes the exine as having "elevated portions between the pits . . ." which "may be reticulate in certain grains, or they may be in definite ridges or striations with the pits in all stages of alignment or fusion."

The pollen grains of *Toxicodendron*, *Actinocheita*, and *Schinus* are prolate spheroidal (length-width equals 1.01-1.14); grains of *Metopium* are borderline between prolate spheroidal and subprolate (1/w ratio = 1.14-1.33). Grains of *Rhus sensu stricto* are subprolate. All have long polar axes. (See Table 3).

Figures 1-8 show photomicrographs of anacardiaceous grains. Four views of each sample grain are shown: (a) plane surface view (Figs. 1-2) showing sculpturing, (b) longitudinal, equatorial view through costae transversales (Figs. 3-4) showing longitudinal section of a colpus, (c) median optical (Figs. 5-6) view showing section of the exine, and (d) view through the pore (Figs. 7-8) from the inside (lower surface). Surface sculpturing in

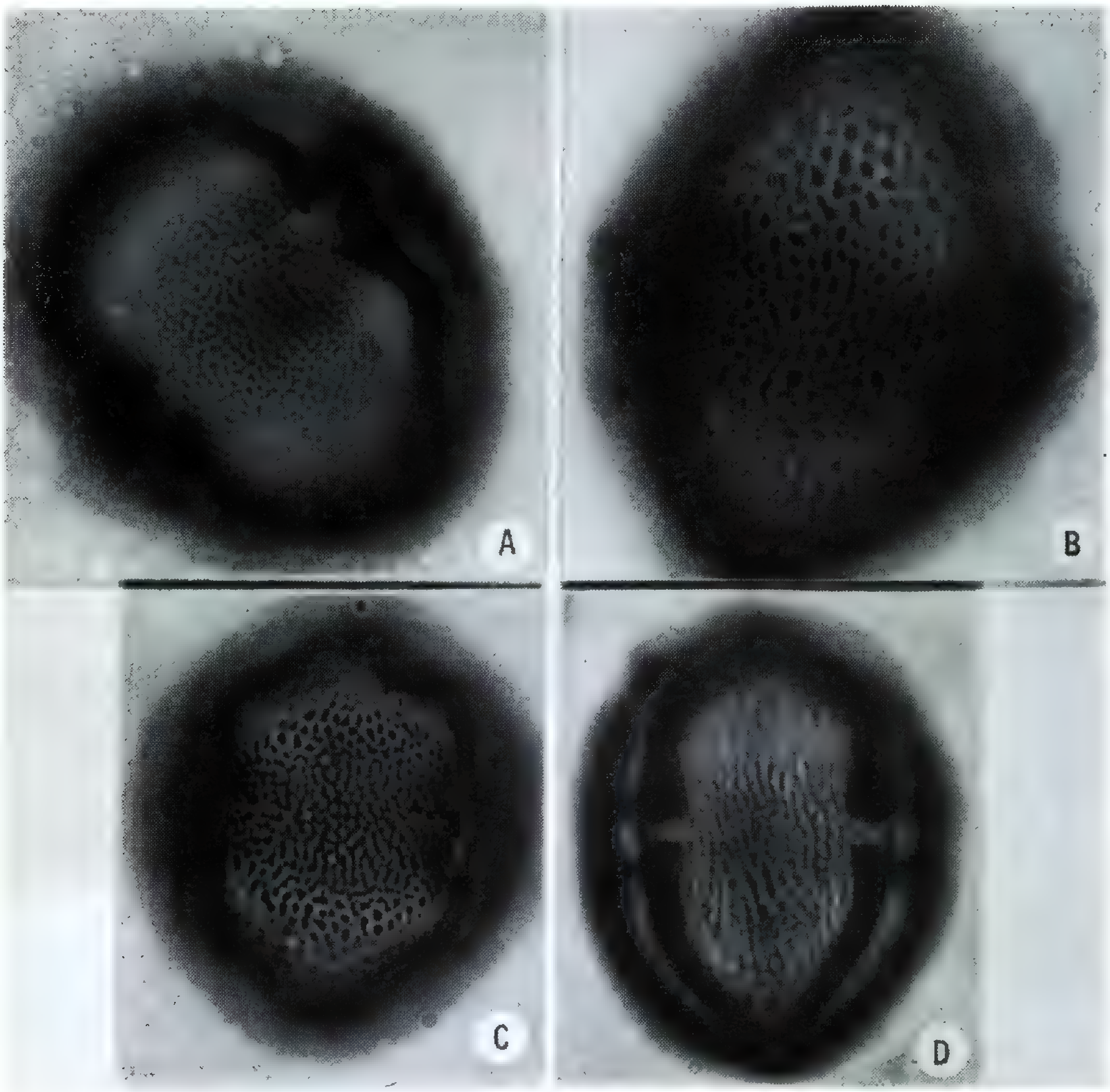

Fig. 1. Anacardiaceous pollen. Surface sculpturing of grains, × 875. A, *Rhus coriaria*. B, *R. copallina* var. *copallina*. C, *Toxicodendron radicans* subsp. *negundo*. D, *T. radicans* subsp. *orientale*.

all grains resembles the surface of a peach pit, seen especially clearly in *Rhus copallina*. (See Fig. 1).

There are few differences among the pollen grains studied which might be useful in classification, except for size (See Table 3). All have similar "peach-pit" sculpturing on the surface. In *Rhus copallina* and *R. glabra* the internal ribs (costae) tend to be more tapering toward the poles of the grain than they do in *R. coriaria* and *R. typhina*, but these differences are only a matter of degree. *Toxicodendron rydbergii* has ribs which arch more broadly toward the poles than do those of other members of the genus which

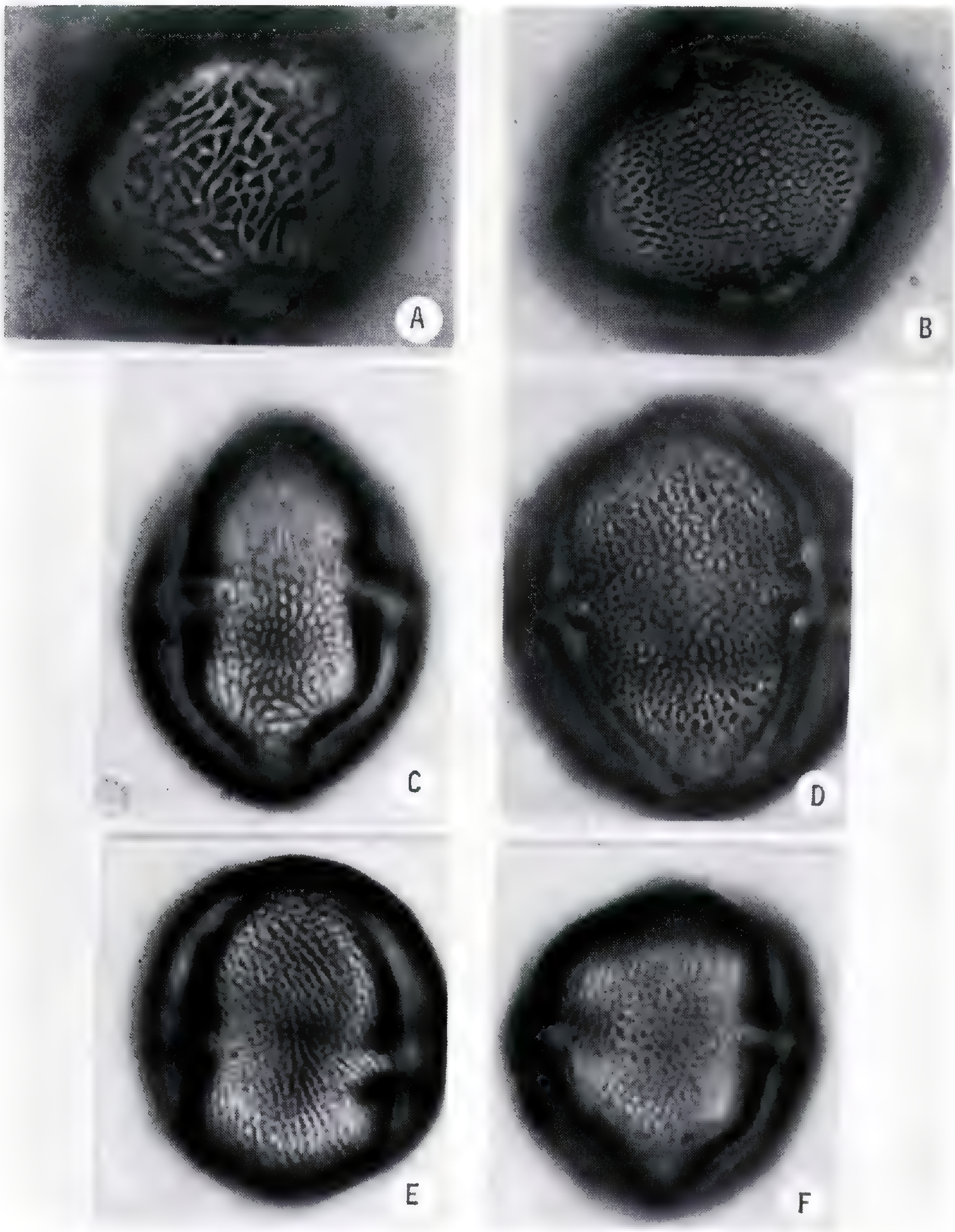

Fig. 2. Anacardiaceous pollen. Surface sculpturing of grains, × 875. A, *Toxicodendron diversilobum*, aberrant grain. B, *T. diversilobum*, normal grain. C, *T. toxicarium* from Florida. D, *T. trichocarpum*. E, *T. rydbergii*. F, *Actinocheita filicina*.

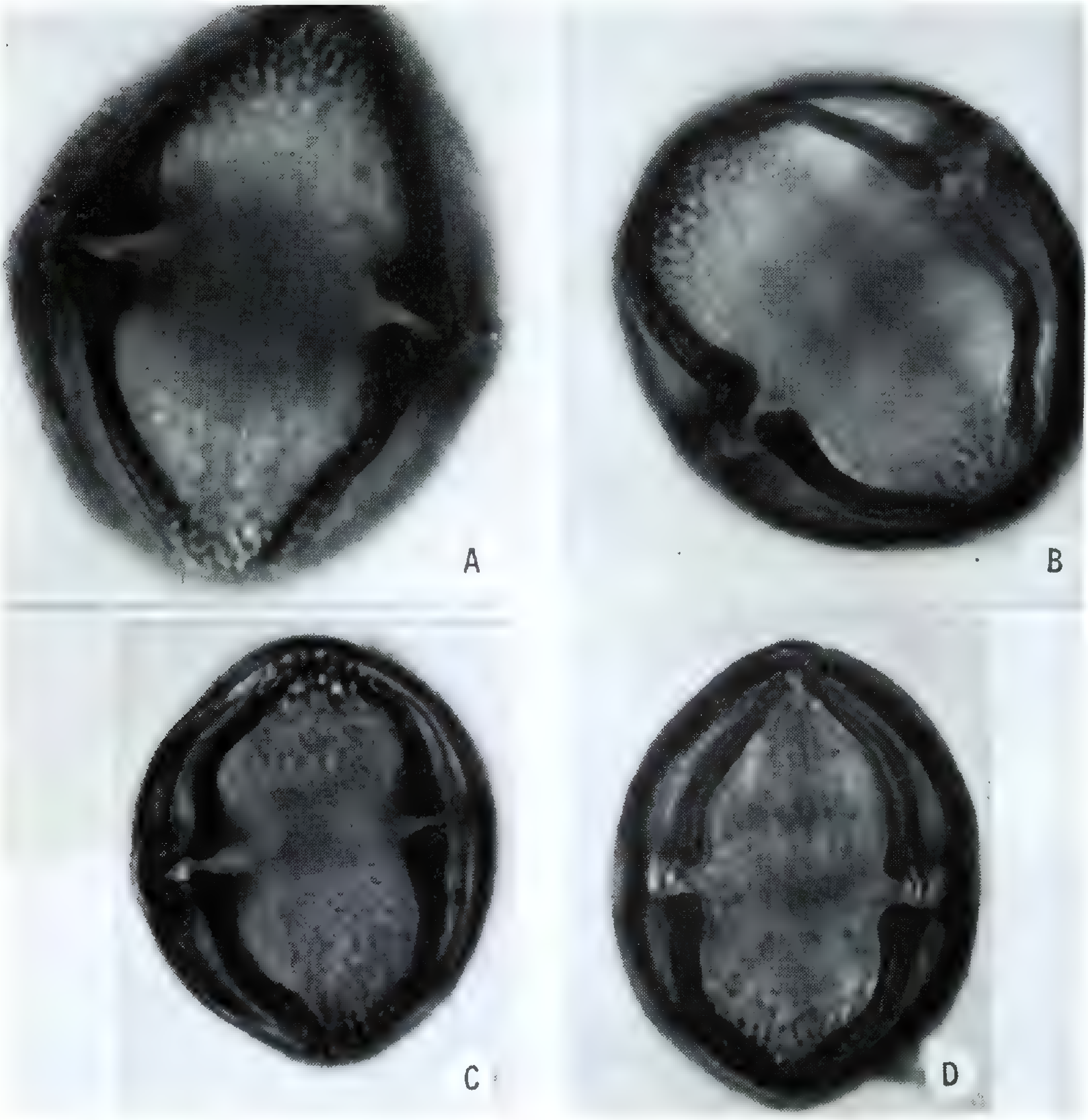

Fig. 3. Anacardiaceous pollen. Section through lateral pores showing costae transversales, × 875. A, *Rhus copallina* var. *copallina*. B, *R. coriaria*. C, *Toxicodendron radicans* subsp. *radicans*. D, *T. radicans* subsp. *orientale*.

were examined. The ribs of *Metopium* appear to arch considerably less (i.e.. more angularly) than those of other genera studied.

A major difference in size is noted between grains of *Rhus* and *Toxicodendron*, yet there remains a consistency within each group. The mean length of the *Rhus* grains studied here is 39.11μ, whereas that for *Toxicodendron* is 26.6μ; among 285 grains which were measured, only three had lengths which overlapped the range of grain size in

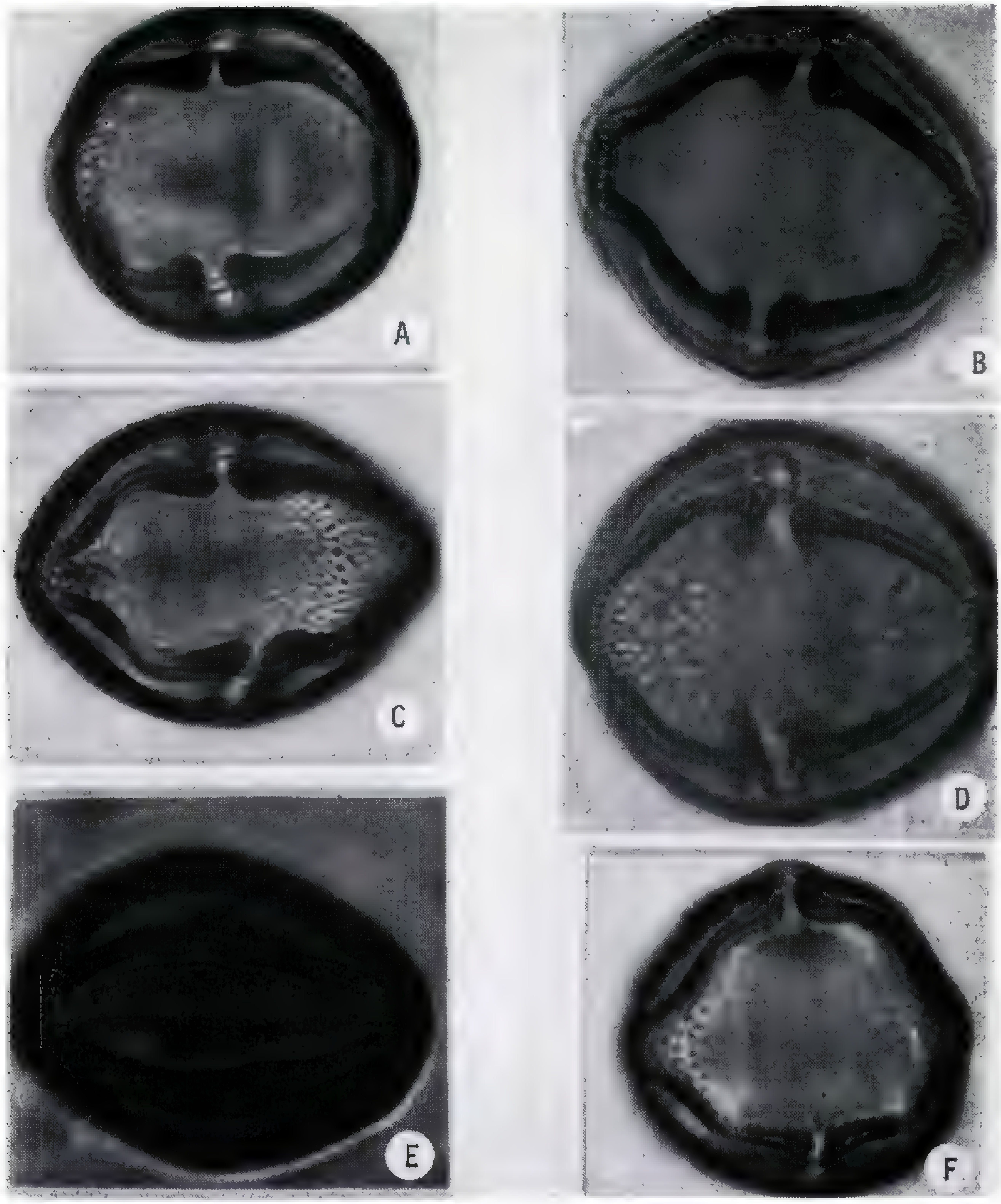

Fig. 4. Anacardiaceous pollen. Section through lateral pore showing costae transversales, × 875. A, *Toxicodendron rydbergii.* B, *T. diversilobum.* C, *T. toxicarium.* D, *T. trichocarpum.* E, *Metopium toxiferum.* F, *Actinocheita filicina.*

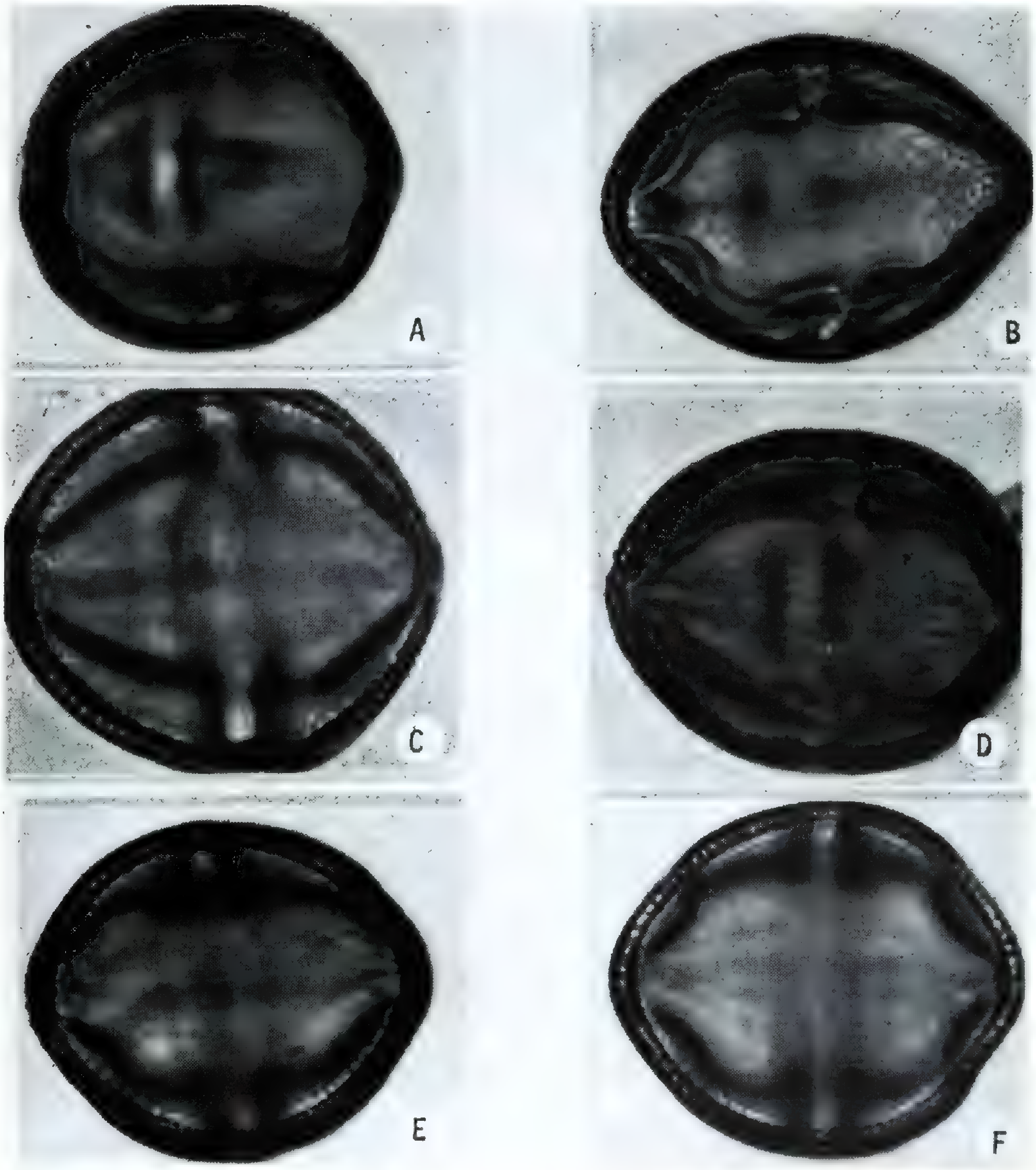

Fig. 5. Anacardiaceous pollen grains. Median section showing wall structure, × 875. A, *Toxicodendron rydbergii*. B, *T. toxicarium* from Florida. C, *T. trichocarpum*. D, *T. radicans* subsp. *orientale*. E, *T. radicans* subsp. *radicans*. F, *T. radicans* subsp. *negundo*.

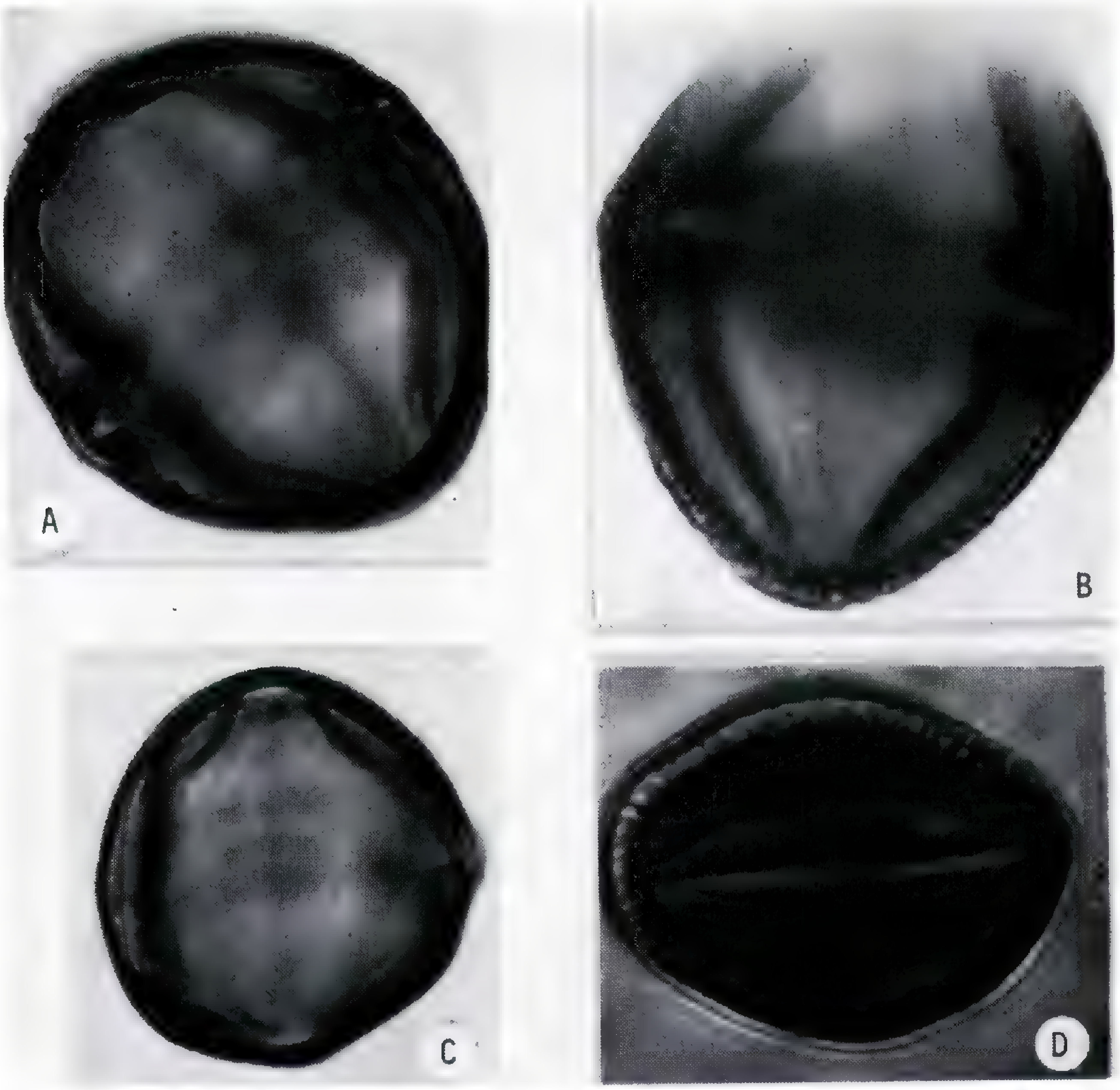

Fig. 6. Anacardiaceous pollen grains. Median section showing wall structure, × 875. *A*, *Rhus coriaria*. B, *R. copallina* var. *copallina*. C, *Actinocheita filicina*. D, *Metopium toxiferum*.

the other genus. By inspection, one may see the clear-cut separation of the samples. Likewise, the mean width of *Rhus* grains studied is 31.71μ whereas that for *Toxicodendron* is 22.84μ. Here 18 grains overlapped the range of widths, so that the separation, though marked, is not so clear-cut as that for the lengths. Kuprianova (1965) found a specimen of *Rhus semialata* (= *R. javanica*) for which the pollen polar axis was 32.4-43.2μ and the equatorial diameter was 25.2-41.8μ as contrasted with *Toxicodendron orientale* (= *T. radicans* subsp. *orientale*) whose length through the polar axis was 28.8-29.3μ and equatorial diameter was 21.6-28.8μ. Wodehouse (1932) measured *Rhus*

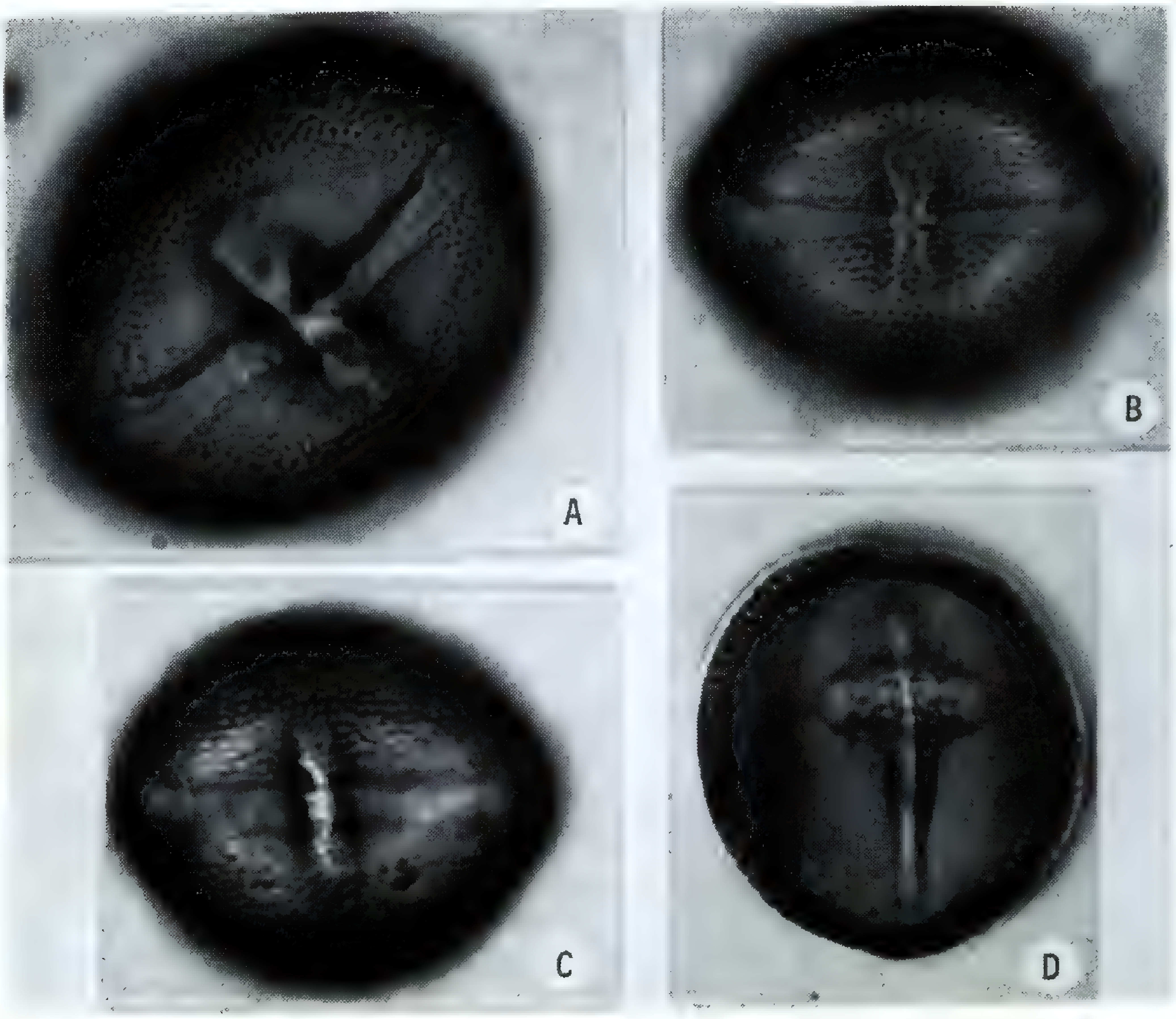

Fig. 7. Anacardiaceous pollen grains. Surface plan view showing pore and colpus, × 875. A, *Rhus coriaria*. B, *Toxicodendron radicans* subsp. *negundo*. C, *T. radicans* subsp. *radicans*. D, *T. rydbergii*.

typhina pollen length as 37.5-39μ and *R. glabra* as 35.3-40μ. Erdtman (1934) measured *R. typhina* pollen as having length 53μ × width 35μ. Kuprianova (ibid.) further describes *Rhus* pollen as having a slit-type pore vs. the oblong pore of *Toxicodendron*; she also calls the sculpturing of *Toxicodendron* grains more patterned (streaming) than those of *Rhus* ("barely noticeable streaming sculpture"), i.e., there are more likely to be rows of markings.

The fact that these differences are significant is of importance to the question of whether or not *Toxicodendron* should be segregated from *Rhus* as a separate genus. The pollen size is certainly not the major factor in settling this controversy, but it lends some weight to the argument that the two should be recognized as separate genera.

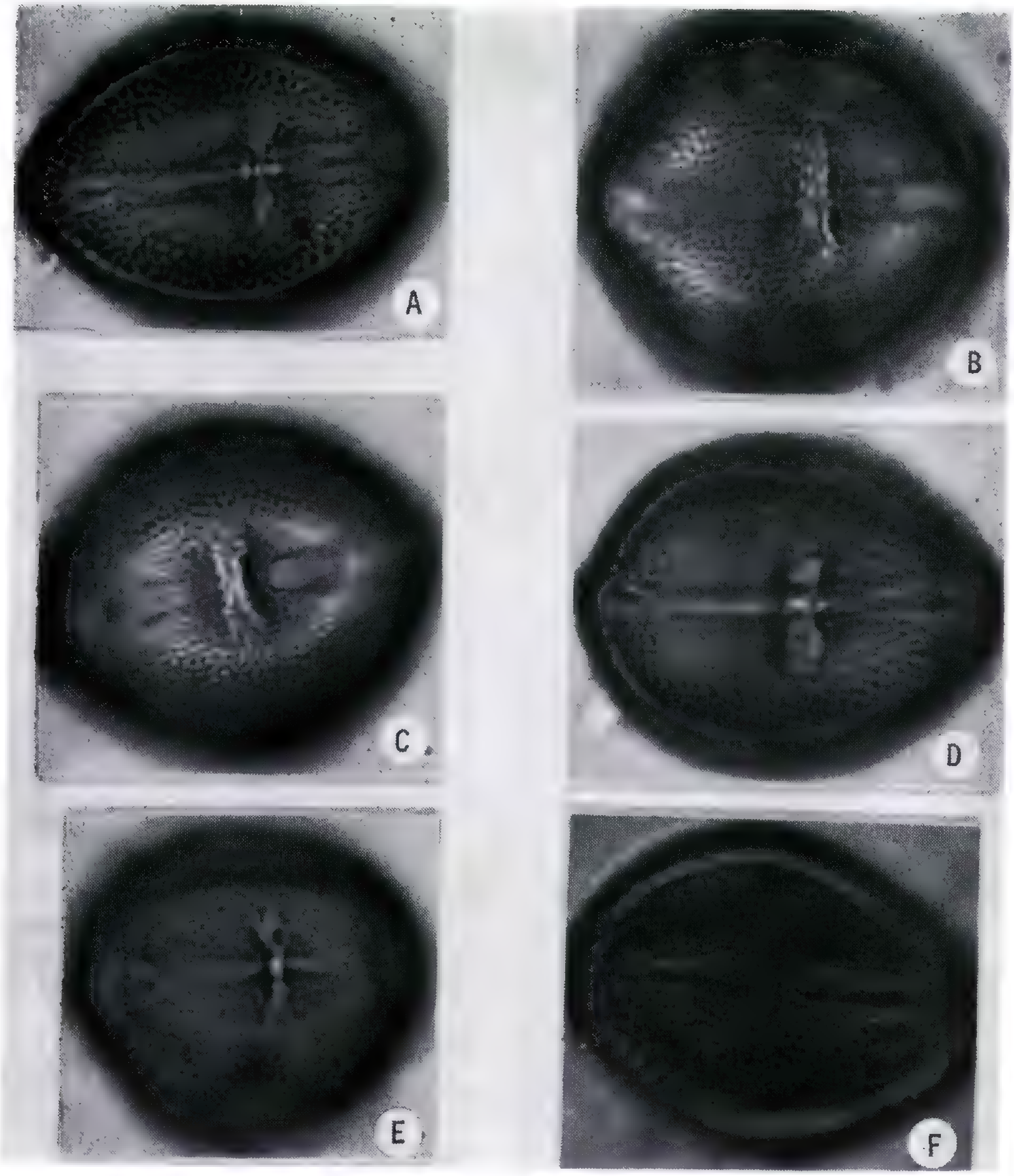

Fig. 8. Anacardiaceous pollen grains. Surface plan view showing pore and colpus. × 875. A, *Toxicodendron toxicarium* from Florida. B, *T. trichocarpum*. C, *T. diversilobum*. D, *T. radicans* subsp. *orientale*. E, *Actinocheita filicina*. F, *Metopium toxiferum*.

Where pollen grains of two different populations of the same taxon were measured (e.g., *Toxicodendron toxicarium*, and *T. radicans* subsp. *radicans*), there was close agreement in size between the two populations. The grains of *T. diversilobum*, *T. vernix*, *T. trichocarpum*, *T. borneense*, *T. radicans* subsp. *orientale*, and *T. rydbergii* are larger

(longer and broader) than grains of other *Toxicodendron* taxa. The smallest grains to be measured were found in *Schinus molle*; these grains are also most nearly spherical (l/w ratio = 1.0). Ikuse (1954) found significantly larger grains of *Rhus ambigua* (= *T. radicans* subsp. *orientale*) than are reported here: 28.5-32.5μ × 27.5-31μ. But Ikuse used glycerin jelly as a mounting medium rather than Canada balsam, claiming that the glycerin jelly caused the grains to swell so that the surface markings might be studied more favorably.

There have been few *Rhus* or *Toxicodendron* pollen grains found in the fossil record. Wodehouse (1932) discovered some *Rhus* pollen in the middle Eocene Green River formation in Wyoming. These grains are very similar to those of *R. typhina* and *R. glabra*, the latter of which grows in that region today. Traverse (1955) described a new species, *Rhus carbogena*, based solely on pollen grains found in the Brandon lignites of Forestdale, Rutland County, Vermont. These were Tertiary (Oligocene?) in age and again resemble those of *R. typhina* and *R. glabra*, both of which currently inhabit that region of Vermont. They are smaller than grains of either extant species, but fall within the range of *Rhus* pollen sizes reported here.

FOSSILS OF TOXICODENDRON

As with most taxa, the fossil record for the poison-ivy complex is incomplete. A study of some fossils from this group of plants and the taxa they represent gives some indication of the past history of the group. The discussion will center around plants listed in Fossilium Catalogus (Edwards and Wonnacott, 1935) and more recently described fossil species. Each will be discussed, evaluated as a member of this complex, and its affinities determined, where possible.

Rhus and its relatives are found frequently in the fossil state in various periods of the Tertiary (Saporta, 1888).

They are never represented by more than detached leaflets and are therefore difficult to determine accurately. The fossils suspected of belonging to this group, or for which discussion is relevant, will be discussed.

Rhus quercifolia Goeppert (1855). Fig. 9.

This name is probably synonymous with *R. aegopodiifolia* Goeppert, Fig. 9. The fossil specimens come from the Tertiary of Bohemia and southwestern Russia (Kryshtofovich, 1914). The material illustrated does not resemble anything in the modern poison-ivy complex, especially that which has previously been called *Rhus quercifolia auct. pl.* and which is herein called *Toxicodendron toxicarium*. The palmate venation shown in Goeppert's illustration reveals five main veins with the lowest two leading to a pronounced lobe on each lateral leaflet, unlike present-day poison-ivy or poison-oak. Specimens which were presumably deposited in Breslau have not been located and are presumed to have been destroyed during World War II.[9]

Kräusel (1919), however, throws some light on the subject. He discusses Goeppert's plants (while citing his own name as author of the binomial) from Silesian collections by Perusch. His illustration (See Fig. 10) is more suggestive of Eastern poison-oak *(Toxicodendron toxicarium)* than is any illustration by Goeppert. The rounded lobes of the terminal leaflet very closely resemble those on leaves of modern Eastern poison-oak, as do the cuneate leaflet bases. The venation also agrees with patterns on modern leaves.

Kräusel felt that his fossil plant was not conspecific with the plant of North America. Until his specimens can be studied more thoroughly, one must consider this fossil as a doubtful member of the poison-ivy complex.

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[9]Personal communication from Dr. Bohnslav Fott, Head of Katedra Botaniky Prirodovedecke Fakulty University Karlovy, 1963.

Fig. 9. Fossil species: *Rhus quercifolia* Goepp. (upper) and *R. aegopodiifolia* Goepp. (lower), (Goeppert, 1855).

There are a number of genera which presumably occupied the region of the Tethys Sea, several of which also extended to eastern Asia (e.g., *Liquidambar, Juglans, Salix,* and *Diospyros*). Some genera of these floras apparently vanished with the tectonic activity that was associated with the uplift of the Alps. The Pliocene vegetation of western Europe is distinguished by the occurrence of a large number of elements no longer a part of European vegetation, but identical with species now living in China, Japan, and North America (Seward, 1931). The close morphological link of *Rhus coriaria* of Europe and *R. michauxii* of the southeastern United States may be an example of plants in the *Rhus* complex that may have once had a range which included both North America and southern Europe. Section *Toxicodendron* may also have shared a distribution in Europe and North America at this time, represented by a fossil which Kräusel illustrated (Fig. 10), a plant now extinct in Europe, possibly as a result of mountain building. Current thinking among European paleobotanists, however, places *Rhus quercifolia* Goeppert in the fossil genus *Monopleura* (Aceraceae). Whether this plant is really the same one which Kräusel had under consideration is not certain.

The binomial *Rhus quercifolia* was listed in synonymy by Steudel (1821) for Eastern poison-oak, earlier than Goeppert's publication; but publication in synonymy does not constitute valid publication according to the Code (Lanjouw, *et al.,* 1966). Therefore, Goeppert's name is valid and is ascribable to him. Unless one regards the Goeppert fossil as conspecific with modern Eastern poison-oak, this binomial combination cannot be used for the modern plants, even by those who believe them to be *Rhus* species and not *Toxicodendron* species.

Rhus toxicodendroides Pilar (1883)

This specimen comes from the Miocene of Croatia. Pilar's plate shows but a single lanceolate acuminate leaf (leaflet?) that is irregularly dentate and slightly asymmetrical. He described it as recalling the form and venation of "*Rhus*

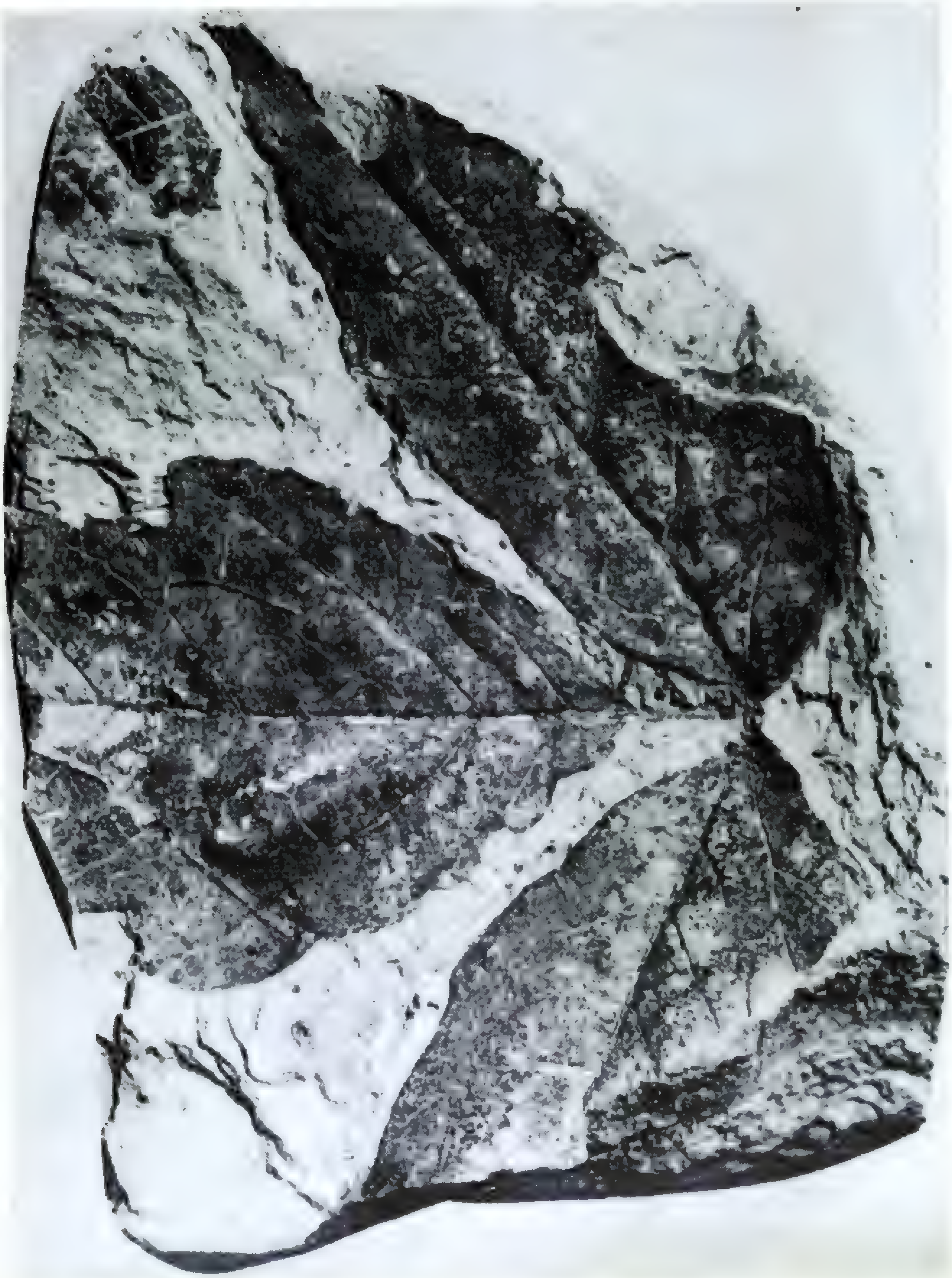


Fig. 10. *Rhus quercifolia* Goepp. from specimens shown in Kräusel (1919).

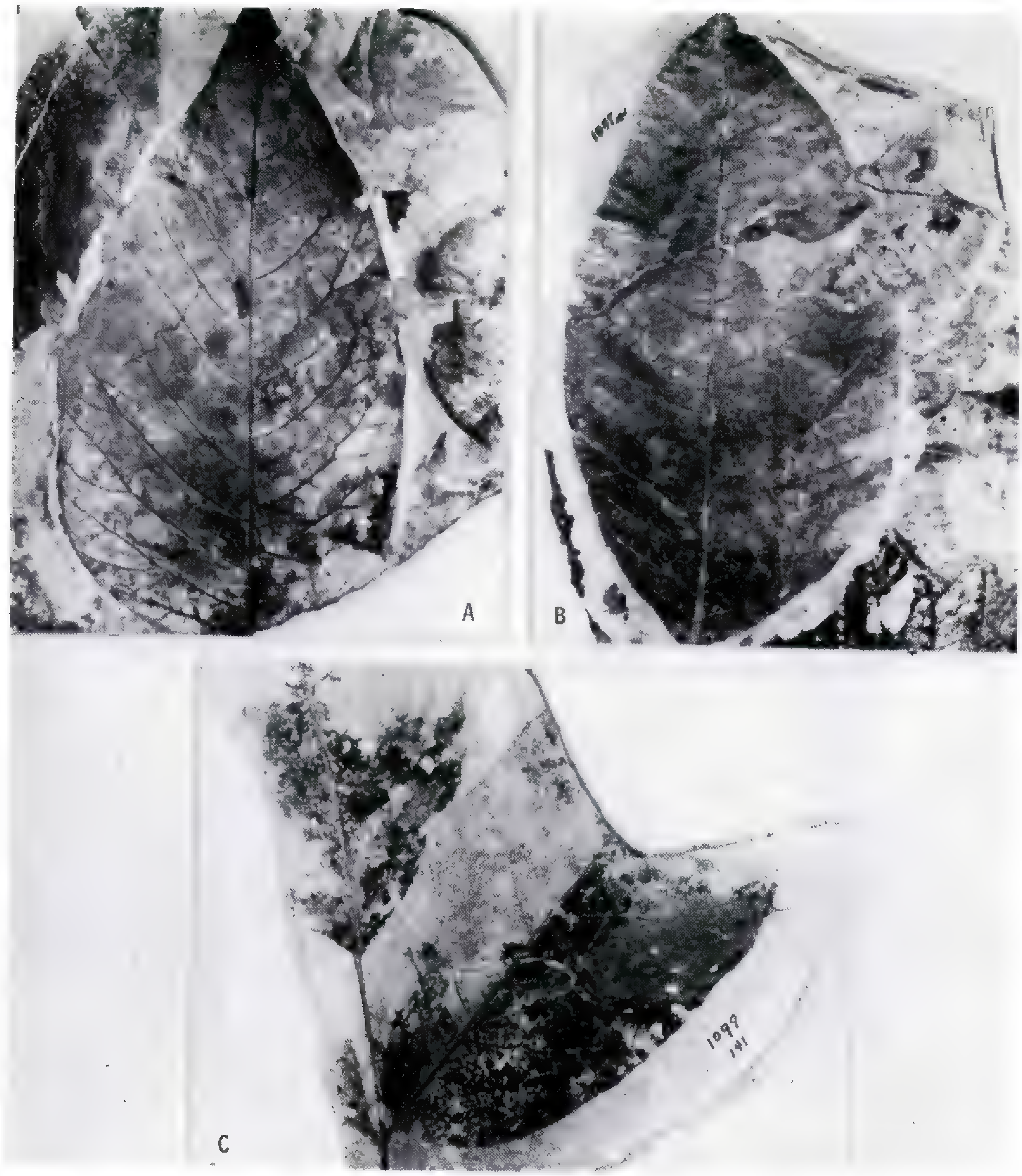


Fig. 11. *Toxicodendron magnifolium* (MacGinitie) Gillis from the Weaverville flora at Redding Creek, California. Specimens at the University of California, Dept. of Paleontology. A, Holotype of *T. magnifolium*, based on *Rhus magnifolia*. Presumably the right lateral leaflet. B, Left lateral leaflet of *T. magnifolium*. C, Specimen showing three leaflets.

Fig. 12. Comparison of fossil and modern poison-ivy. Upper: Close-up view of venation pattern of *Toxicodendron magnifolium* (from holotype). Lower: Close-up view of venation pattern of *T. radicans* subsp. *orientale* (from Gillis 4691, Japan).

Toxicodendron L. of North America." It probably is not related to any extant *Toxicodendron* and is difficult to place even in the Anacardiaceae. The type cannot be found at the Geological Paleontological Museum at Zagreb where Pilar's specimens are located. although other *Rhus* species described at the same time are there.[10]

Toxicodendron magnifolium (MacGinitie) Gillis, comb. nov. Fig. 11.

Rhus magnifolia MacGinitie, Publ. Carnegie Inst. Wash. 465: 144. 1937. Type: *Harry D. MacGinitie s.n.*, California, Trinity County, Oligocene beds at Redding Creek; Weaverville flora. (University of California, Dept. of Paleontology, holotype; several isotypes).

This fossil plant shares with modern poison-ivy (especially the group including *Toxicodendron radicans* subsp. *radicans*, *hispidum*, and *orientale*) several morphological characteristics. Dr. MacGinitie noted the close resemblance of the fossil to leaves of Japanese poison-ivy (*T. radicans* subsp. *orientale*), a resemblance that is closer than with North American taxa today (Fig. 12). The fossil suggests a link between Asiatic poison-ivy and North American populations. Aside from the possibility of long-distance dispersal as a mechanism of accounting for poison-ivies in Asia and North America, some ancient population may have existed continuous across the Alaskan-Siberian land bridge during the Paleocene-Eocene interval. There are unfortunately no fossils from the northern Orient, the Aleutians, Alaska, or western Canada to sustain the hypothesis that the plants really had this distribution.

The fossil associates of *Toxicodendron magnifolium (Ilex, Nyssa, Juglans,* and *Taxodium)* are similar to poison-ivy's present-day associates in the southeastern United States, and it may actually represent an organism whose ecological requirements are little changed now. The fossil specimen,

[10]Personal communication from Dr. Ivan Crnolatac, Curator of the Geological Paleontological Museum, Zagreb, Jugoslavia, 1962.

however, was found in a region not presently inhabited by poison-ivy, but rather by western poison-oak, *T. diversilobum.* Because of the great separation in time and distance between the fossil and modern plants, I choose to recognize the taxon named by MacGinitie as distinct from the modern plants, but nevertheless to transfer the species from *Rhus* to *Toxicodendron* to place it with the toxic sumacs.

Toxicodendron lobatum, the western poison-oak, has been found also in fossil forms.

Rhus diversiloba first reported by Potbury (1932) in Pleistocene deposits at San Bruno, California. Her specimens are seeds with obtuse ends and irregular nodules 5.5 × 3 mm. (Univ. Cal. Coll. Pal. Bot. Plesiotype 437). The modern seed measures 5-6 × 3.4-4 mm. Fruit characters of taxonomic significance are all found in the evanescent exocarp which is not available in the fossils. Wood fragments were reported by Mason and Chaney (1933) from Carpinteria, California, in asphalt sand. The accompanying fossil vegetation was a Monterey pine forest. Such forests are now found 200 miles farther north, suggesting that the plant grew during a glacial (vs. interglacial) epoch when the lower latitudes were colder than they are today. The wood fragments are rare. Both those records were too fragmentary to determine the materials with certainty.

More seeds were reported by Mason (1934) in the Tomales formation of the Pleistocene near Inverness Bay (Mason's locality 609). The soft mesocarp and exocarp were lost, but the hard endocarp persisted (Univ. Cal. Coll. Pal. Bot. Plesiotype 514). Other plants found with it (*Rubus spectabilis, Symphoricarpos, Pseudotsuga,* and *Acer macrophyllum*) are frequent associates of *T. diversilobum* today in northern California, Oregon, and Washington. Based on fossil invertebrates also present, this plant must have grown during an interstadial period warmer than today, in a vegetation related to the closed-cone pine forests now discontinuously relict along the coast (Mason, 1934).

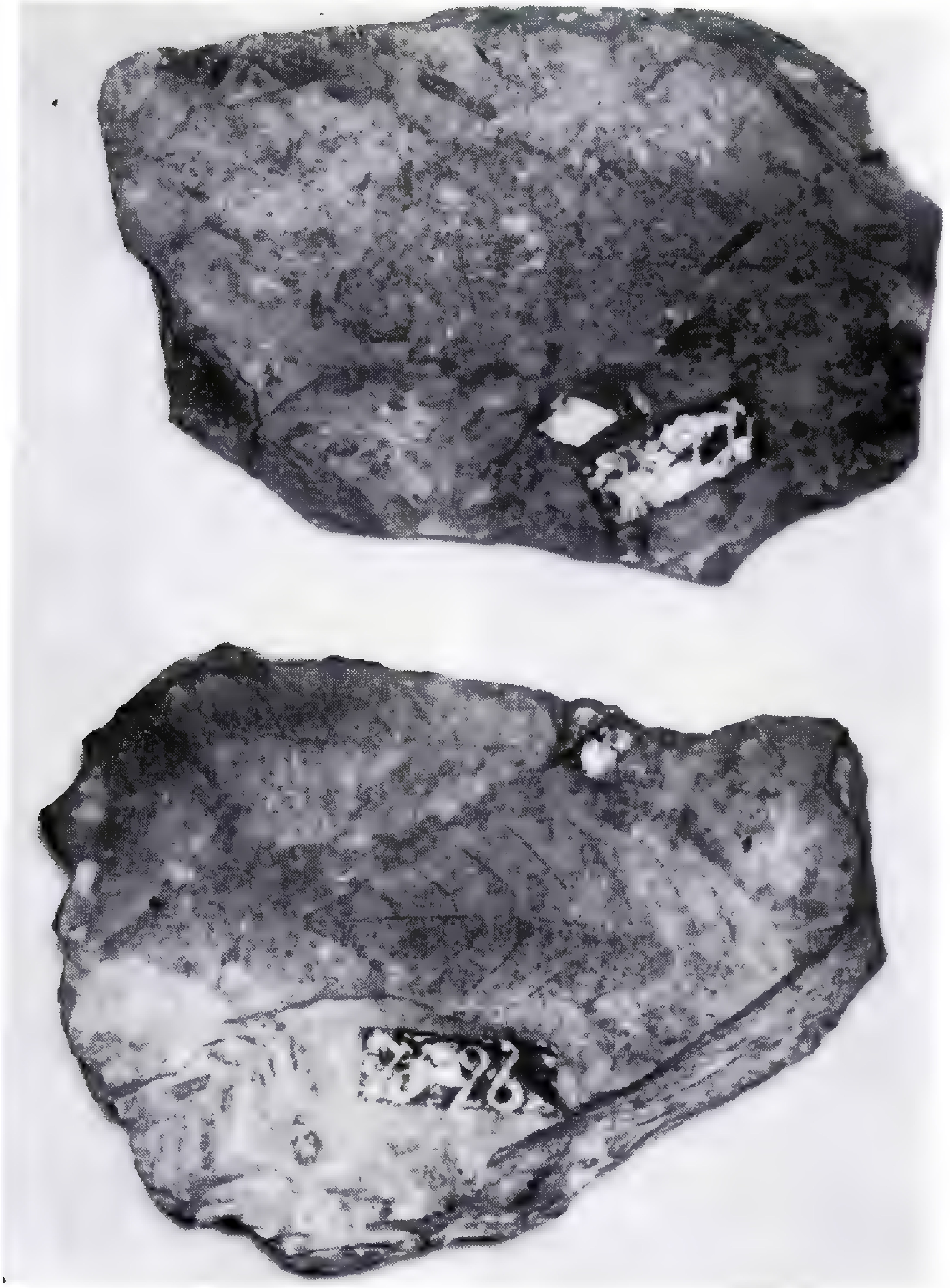
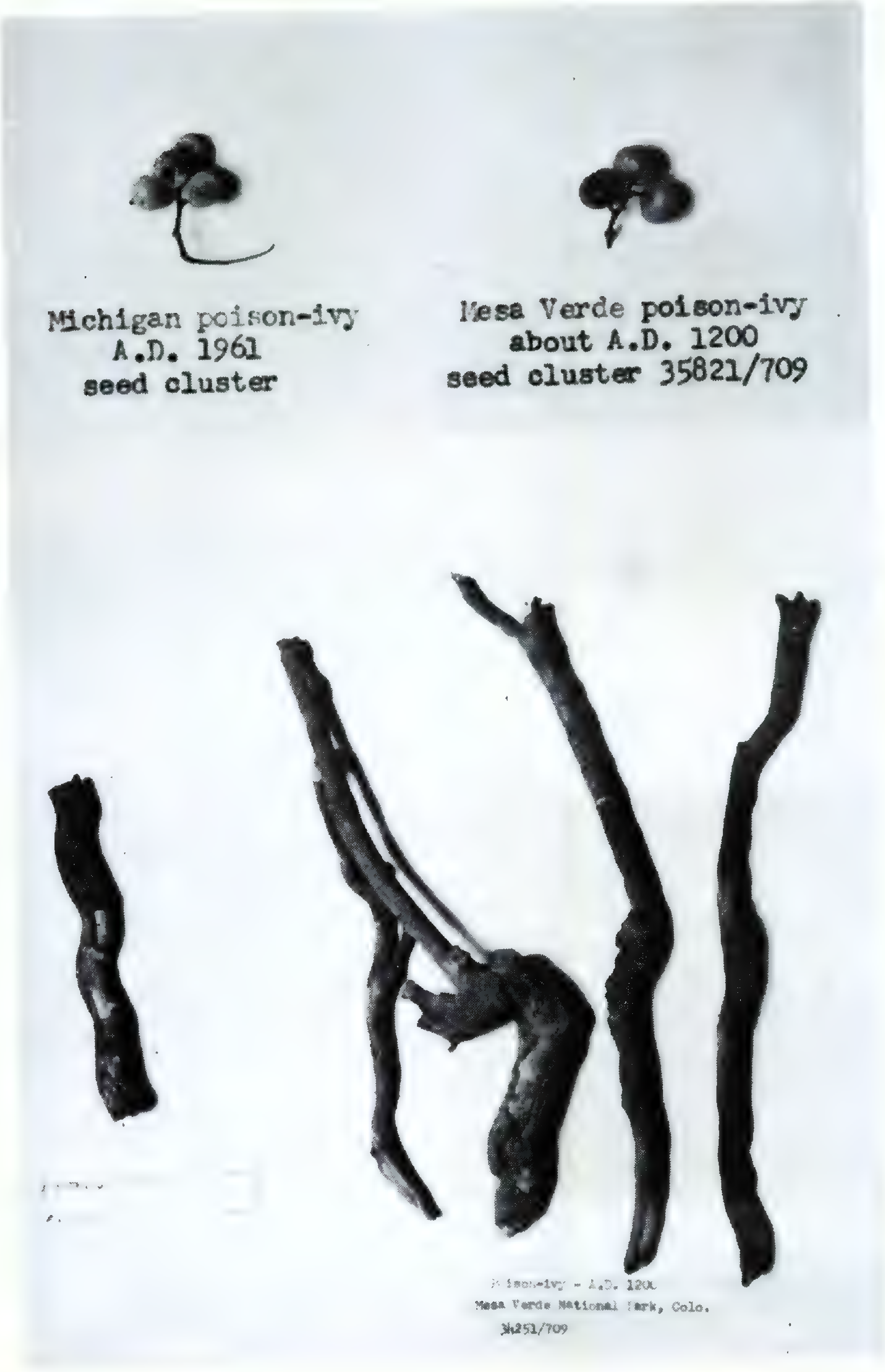


Fig. 13. *Quercus applegatei* Knowlton (1900) (from type collection, United States National Museum).

Fig. 14. Archeological remains. Upper: *Toxicodendron rydbergii,* from Mesa Verde, ca. A.D. 1200 (right), from Wexford County, Michigan, 1961, for comparison (left). Lower: Roots and stems from cliff dwellings at Mesa Verde National Park, Colorado (specimens courtesy of the Wetherill Archaeological Project, Douglas Osborne, Director), see text.


Michigan poison-ivy
A.D. 1961
seed cluster
Mesa Verde poison-ivy
about A.D. 1200
seed cluster 35821/709
Mesa Verde National Park, Colo.

Quercus applegatei Knowlton (1900). Fig. 13.

This species has been mentioned as a possible Anacardiaceous plant related to *Toxicodendron diversilobum*. A careful examination was made of specimens from the type collection (at the Department of Paleobiology, Smithsonian Institution) from the Tertiary Ashland beds in Oregon. Most specimens are not Anacardiaceae and probably are *Quercus* (except for one which appeared to be neither Anacardiaceae nor *Quercus*). The leaflet margins of the fossil appear to be bristle-tipped; the lobes are somewhat pointed; there is no evidence that the leaves were compound. This species therefore cannot be recognized to be a *Rhus*, i.e., *Rhus applegatei* (Knowlton) Chaney ex Potbury (1932).

Archeological Remains. Fig. 14. Special note is made of a unique group of specimens which are barely fossils in the strictest sense. They are, however, a group of fruits and stem and root fragments estimated by the Wetherell Project using radiocarbon methods to be about 700 years old, found in adobe dwellings at Mesa Verde National Park, Colorado. The dry desert air and freedom from disturbance have permitted complete preservation of the plant fragments, so that they are still recognizable today. Poison-ivy plant parts are known to be used by modern Indian tribes in various ceremonial ways, customs originating perhaps as far back as 700 years ago.

Several of the stem and root fragments were examined by Dr. Charles Heimsch of Miami University, and determined possibly to be poison-ivy, based on anatomical detail. Most of them, however, were decidedly not poison-ivy. The

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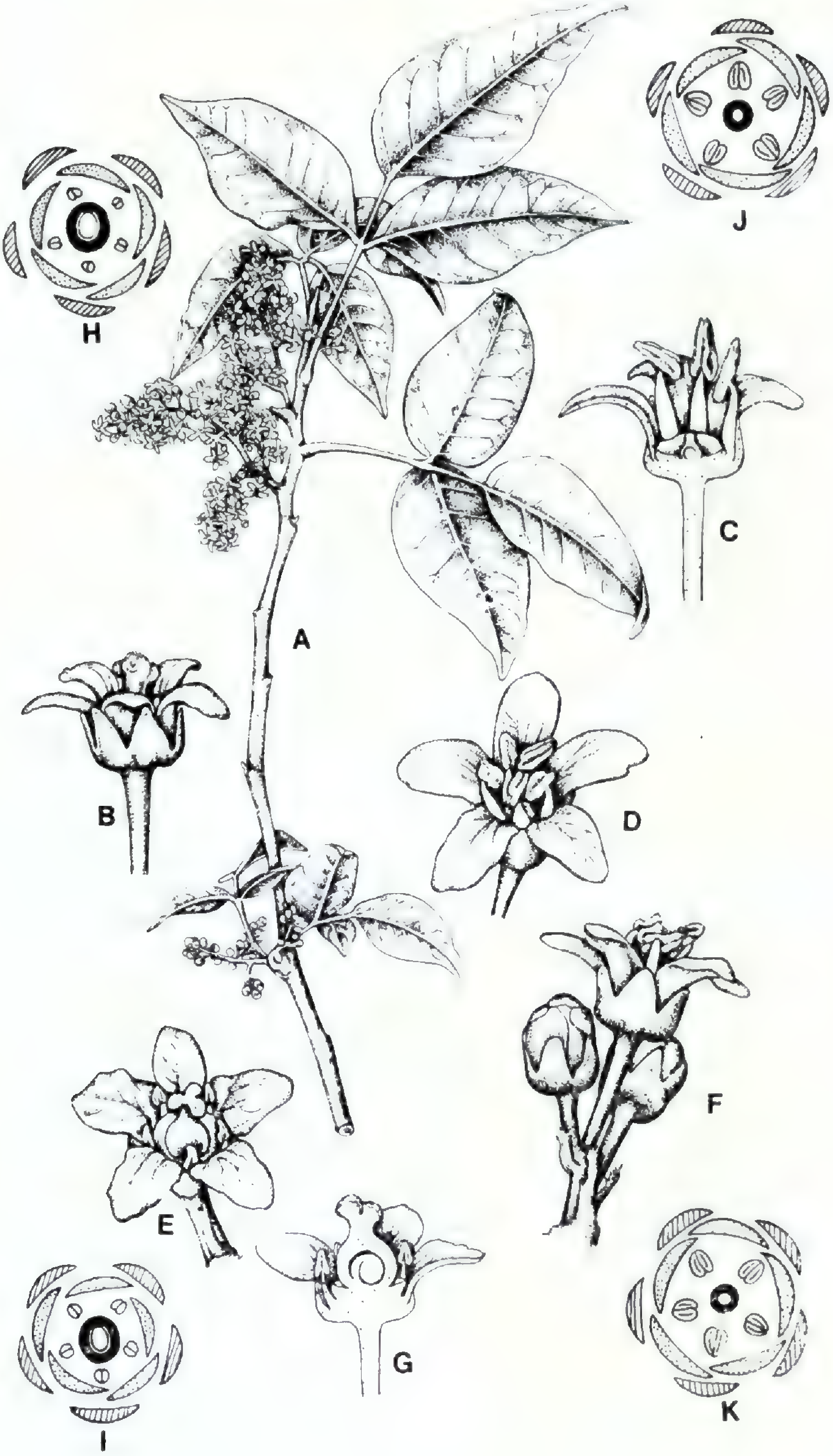
Fig. 15. Flowering *Toxicodendron radicans* subsp. *radicans*, from south Florida (Drawn by Priscilla Fawcett). A, Habit sketch, × 0.33. B, Female flower, × 3.3. C, Male flower, × 3.3. D, Male flower, × 3.3. E, Female flower, × 3.3. F, Ultimate branch of inflorescence, × 3.3. G, Longisection of female flower, × 3.3. H, I, Floral diagrams of alternate forms of aestivation of female flower. J, K, Floral diagrams of alternate forms of aestivation of male flower.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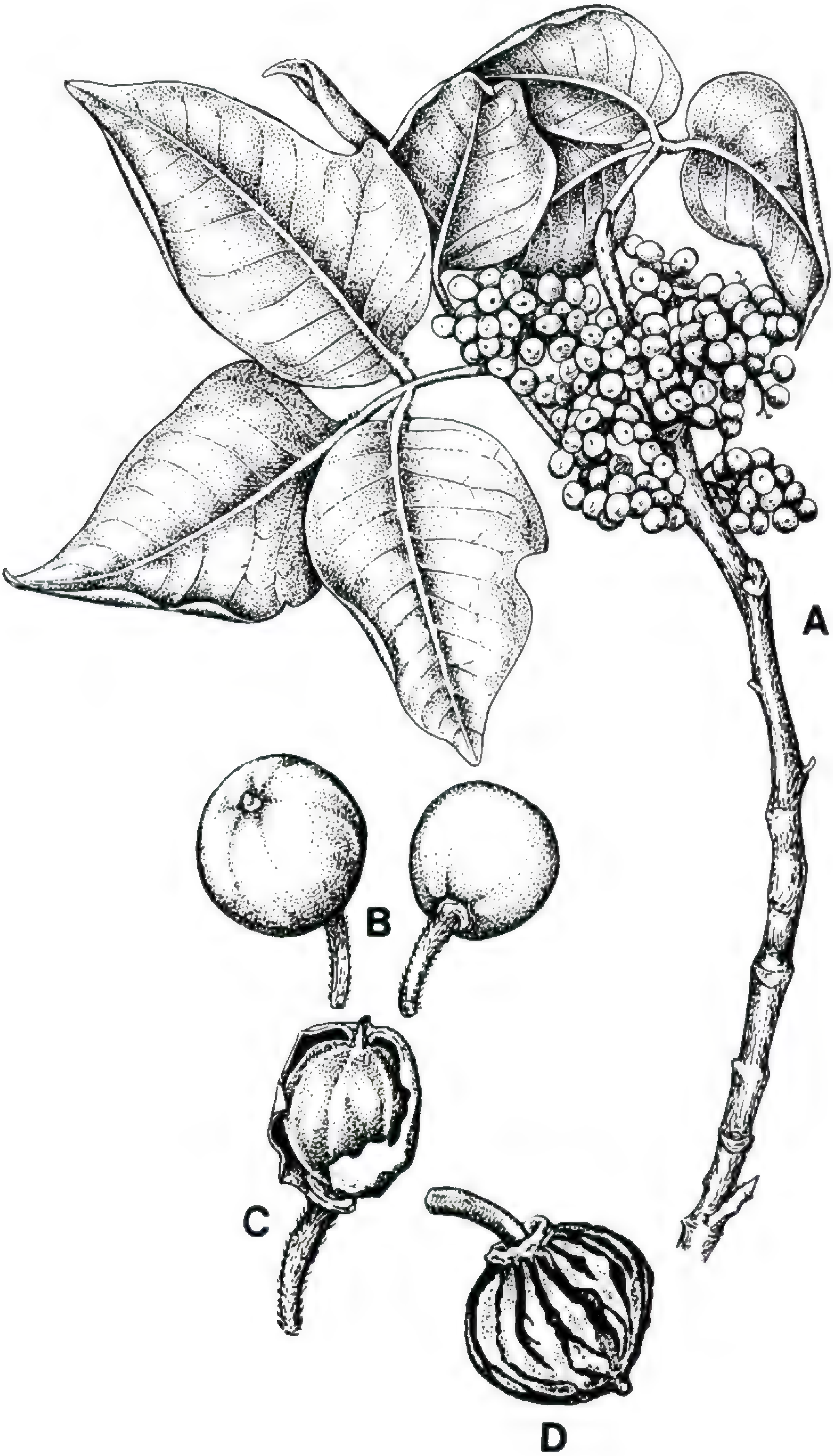
A
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fruits, on the other hand, are unquestionably *Toxicodendron rydbergii*, a taxon which still grows in that vicinity of Colorado.

FLOWER AND FRUIT MORPHOLOGY

Inflorescence. Figs. 15-16.

The flowers of the genus *Toxicodendron* are borne in paniculate or racemose thyrses in the axils of leaves. The ultimate clusters are determinate, of three or four flowers each. The inflorescences are variable in number of flowers; when large, the clusters are pendulous. In fruiting condition, the inflorescence of a few taxa may be erect in small, tight clusters, but will become pendulous in those taxa wherein the inflorescence is large and loose, bending under the weight of the developing fruits. Lignification of the fruiting rachis enables even a heavy cluster to stand erect in some taxa *(T. rydbergii* and *T. toxicarium)*. The bracts of the inflorescence are lanceolate and deciduous. Inflorescences vary from a few cm in length in *T. rydbergii* to over 40 cm in *T. nodosum*.

Flowers. Figs. 15, 17-19.

The entire genus has relatively small, pentamerous flowers which differ more markedly between the sexes of a single species than they do within the same sex throughout the genus. That is to say that one cannot use the flowers for key taxonomic characters except for separating section *Toxicodendron* from *Venenata* on stamen characters.[11] Miller and Martyn (1807) maintained that the male flowers of poison-ivy smelled like lily-of-the-valley, and that the female flowers bore no scent, but I find no evidence to substantiate this.

[11]See discussion of the androecium.

Fig. 16. Fruiting *Toxicodendron radicans* subsp. *radicans*, from south Florida (Drawn by Priscilla Fawcett). A, Habit sketch, × 0.75. B, Intact fruits, × 5.5. C, Fruit with portion of exocarp removed, × 5.5. D, Fruit with exocarp removed, showing striated endocarp; the form of the usual propagule, × 5.5.

Fig. 17. Flowers of *Toxicodendron radicans*. Upper: Cross section of subsp. *negundo*, taken just below midpoint of flower, × 30. Lower: Longisection of subsp. *orientale*, showing perianth parts (note the long reflexed petal), × 80.

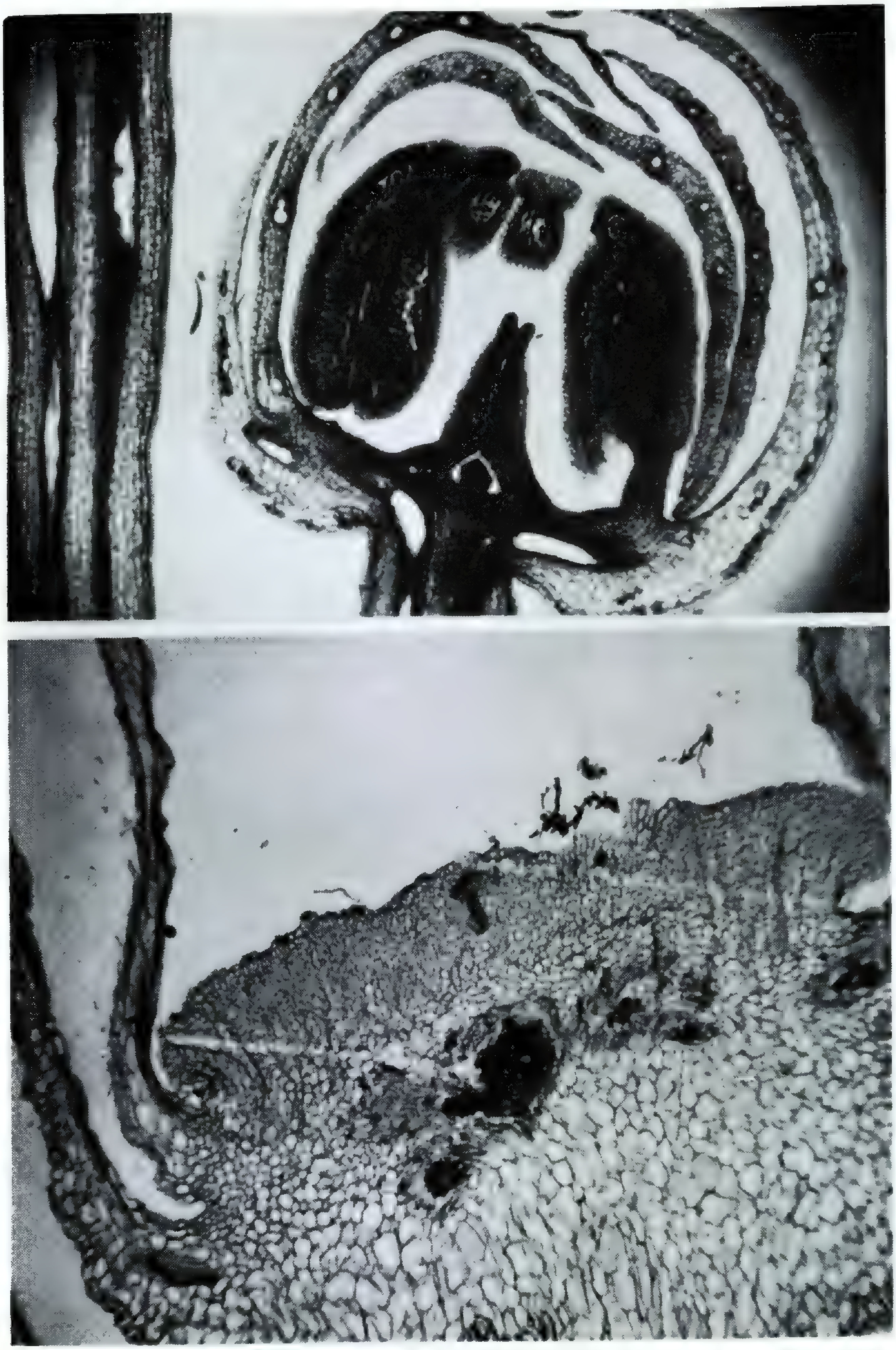

Fig. 18. Longisection of the flower of *Toxicodendron radicans* subsp. *negundo*. Upper: Flower in bud showing stamens, staminal disk and sterile ovary, × 35. Lower: Open flower, showing attachment of petal and sepal to staminal disk, × 90.

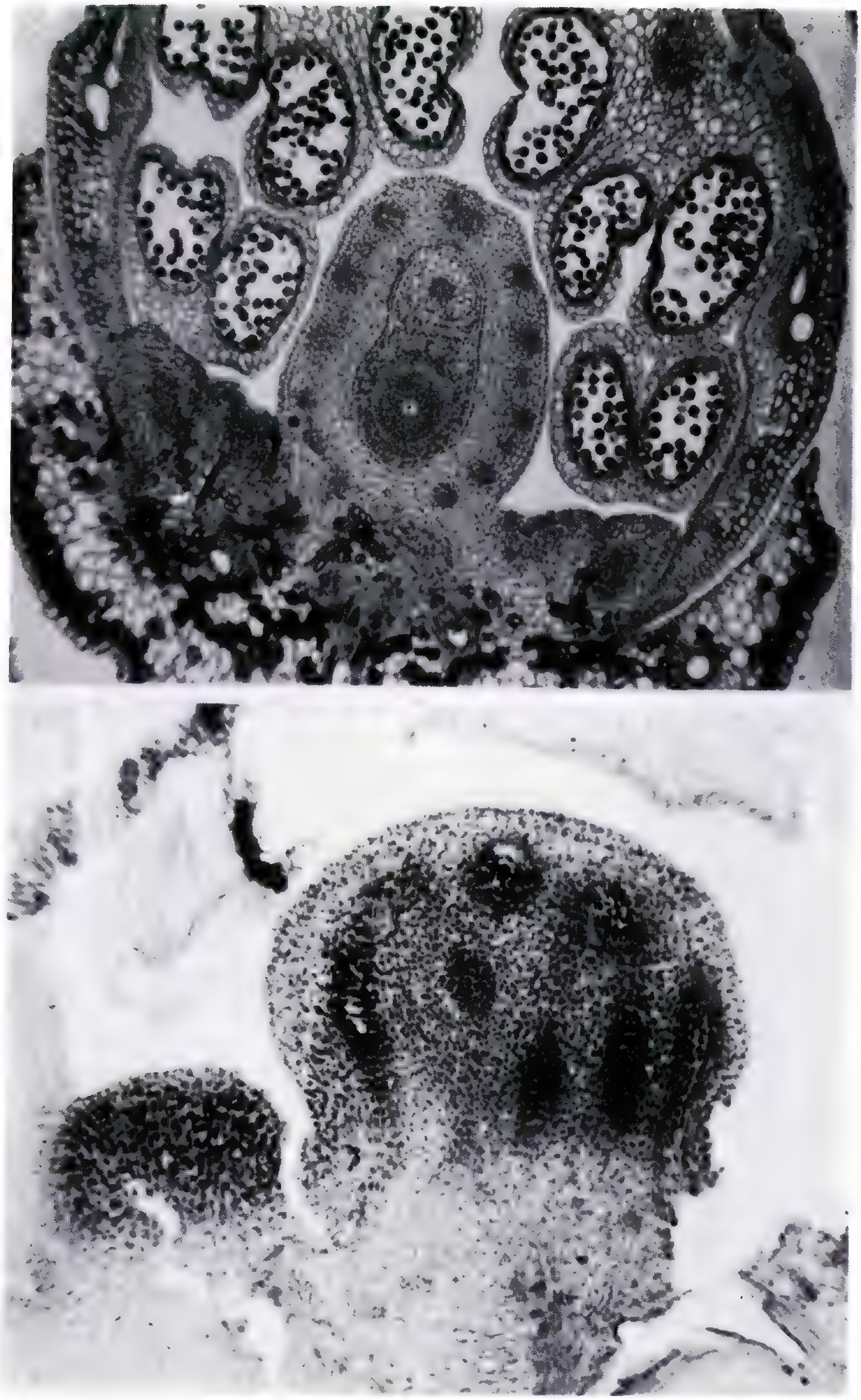

Fig. 19. Longisection of flowers of *Toxicodendron radicans* subsp. *negundo*. Upper: Male flower, showing fertile stamens and developing rudimentary ovary × 85. Lower: female flower, sectioned after petals had fallen, showing enlarging disk and ovary. Dark stained cells in the ovary are incipient resin canals × 65.

Calyx

The five sepals are united only immediately above their insertion below the disk. They are broadly lanceolate or ovate, imbricate in the bud, and do not enlarge significantly once the flowers open. The bases are green, but the upper half is cream-colored like the petals, often with prominent purplish veins. They alternate with the petals. There is a thicker epidermis on the abaxial surface of the sepals than on the adaxial surface, and the outer surface may be slightly pubescent at the base. Resin ducts pervade the phloem of the sepals as they do also in other floral organs. The sepals shrink to dark brown vestiges in fruit, but remain at the base of the staminal disk, and are disseminated with the fruits.

Corolla

The five petals are cream-colored, ascending, glabrous, free, and imbricate in the bud, often with prominent purplish veins. They are obtuse, ovate to lanceolate, always smaller in the female than in the male flowers. In male flowers of Asiatic subspecies of *Toxicodendron radicans* the tips are longer and more prominently reflexed — to over half the total length — than elsewhere in the genus. The shorter petals in female flowers may be slightly recurved, but never reflexed. Poison-carrying resin ducts are found in the phloem of the petals. There is a thick epidermis on both surfaces of the petals. The corolla is attached to the under side of the staminal disk.

Androecium

The five stamens are borne on a glabrous, substaminal disk, typical of Anacardiaceae and related families and orders. Anatomy texts do not treat the origin of this disk, but it appears to have its origin as an outgrowth of the torus. The disk surrounds the ovary, being present to a greater or lesser degree even in female flowers, and is attached to the ovary base. In ripened fruits, the disk and attached calyx remain intact, although shriveled, at the proximal end.

In flowers of sect. *Toxicodendron* the stamens possess

subulate filaments with large, elongate anthers, 4-celled at maturity. They are borne on the edge of the cushion-like disk, alternating with the petals and lobes of the disk. The anthers are oblong, dorsifixed, nearly as long as the filaments, with only the anthers projecting beyond the corolla. Dehiscence is longitudinal and introrse.

Male flowers may be used diagnostically to separate sect. *Toxicodendron* from sect. *Venenata*. The former has stamens included within the perianth at maturity, elongated anthers, and subulate filaments. The latter has stamens exserted at maturity with globose anthers only about one-fourth as long as the enlarged-based filaments. In other characters, the anthers of this section are like those of sect. *Toxicodendron.*

In female flowers, reduced, sterile stamens are present. Microscopic sections show that there is active nuclear division (meiosis?) in progress in these anthers, but they produce no pollen.

Gynoecium

The ovary is tricarpellate, with but one carpel fertile. It is sessile or partially buried in the hypogynous disk. The style is terminal on the ovary, branching near the tip into three parts. The stigma is captitate, simply an expanded portion of the style just above a slight constriction. It may be rough and minutely pitted, but is never pubescent. It turns black when it ceases to function in receiving pollen. This color change from white to black is useful in indicating whether a flower can still be pollinated. The single ovule is anatropous and parietal, seemingly basal, raised on a short, ascending basal funicle.

In male flowers, there is a rudimentary ovary complete with ovule, style, and stigma, although all are reduced in size. The ovary in male flowers begins to develop apparently fertile tissue for a time and even produces rudimentary fruit characteristics such as a thickened ovary wall complete with resin ducts. These parts are deciduous with the flowers when pollination is complete.

In functional female flowers, the ovary wall will enlarge

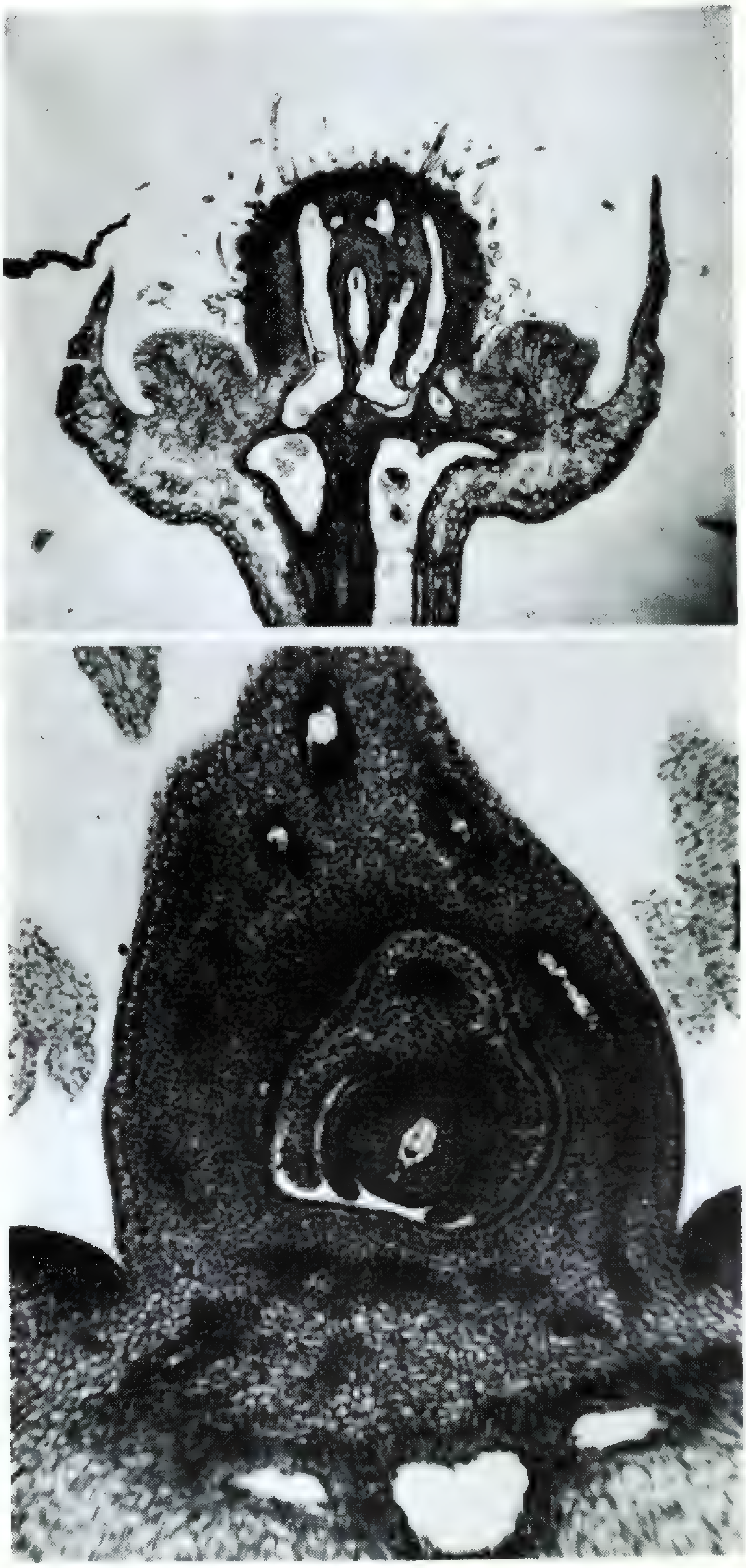

Fig. 20. Longisection of young fruit of *Toxicodendron*. Upper: *T. toxicarium*, showing enlarged disk, calyx remnant, resin canals and hairs on the outer surface, × 25. Lower: *T. radicans* subsp. *negundo*, showing ovule development, × 100.

along with the adjacent hypogynous disk after fertilization. In addition to enlargement, the resin ducts become very prominent in the developing fruit. It is these ducts which make up the striations on the mesocarp of the ripened fruit.

Fruit. Figs. 16, 20-22.

The fruit is a dry drupe with a pericarp that matures into three distinct layers: a brittle, chartaceous exocarp, a fibrous and waxy mesocarp in which are embedded resin canals, and a bony endocarp to which is firmly affixed the seed wall. The drupe is globose in *Toxicodendron radicans* and *T. toxicarium*, but laterally flattened, bilaterally asymmetrical, and with a somewhat acuminate tip culminating in the stigmatic surface in most other species. The bony endocarp develops early in the maturation of the fruit, but the separation of the exocarp occurs only in the later stages of ripening.

The exocarp is green until late stages of development when it turns yellow, straw-, dun-, or cinereous-colored (deep brown in *Toxicodendron wallichii*). It is glabrous in a number of taxa, but may produce non-glandular hairs in others. Any hairs that are produced begin as evaginations of the outer cell layer. In some populations the ripened fruit is papillose rather than pubescent. These papillae are interpreted as incipient or reduced hairs, and are therefore considered along with hairs for taxonomic purposes. The hairs begin as multi-celled, bulbous evaginations, attached by stalk cells, appearing glandular, but developing ultimately into unbranched, multicellular, elongate, bristle-like hairs of varying length. The hairs are scattered to dense in *T. radicans* subsp. *orientale*, subsp. *radicans*, and in *T. toxicarium*. There are much finer, almost setose hairs in *T. diversilobum* but very dense, elongate, and bristly trichomes in *T. radicans* subsp. *hispidum*, reaching a length of nearly a millimeter in the latter taxon. The trichomes appear to be hollow at maturity, unlike the leaf trichomes which often appear to be filled with a dark-

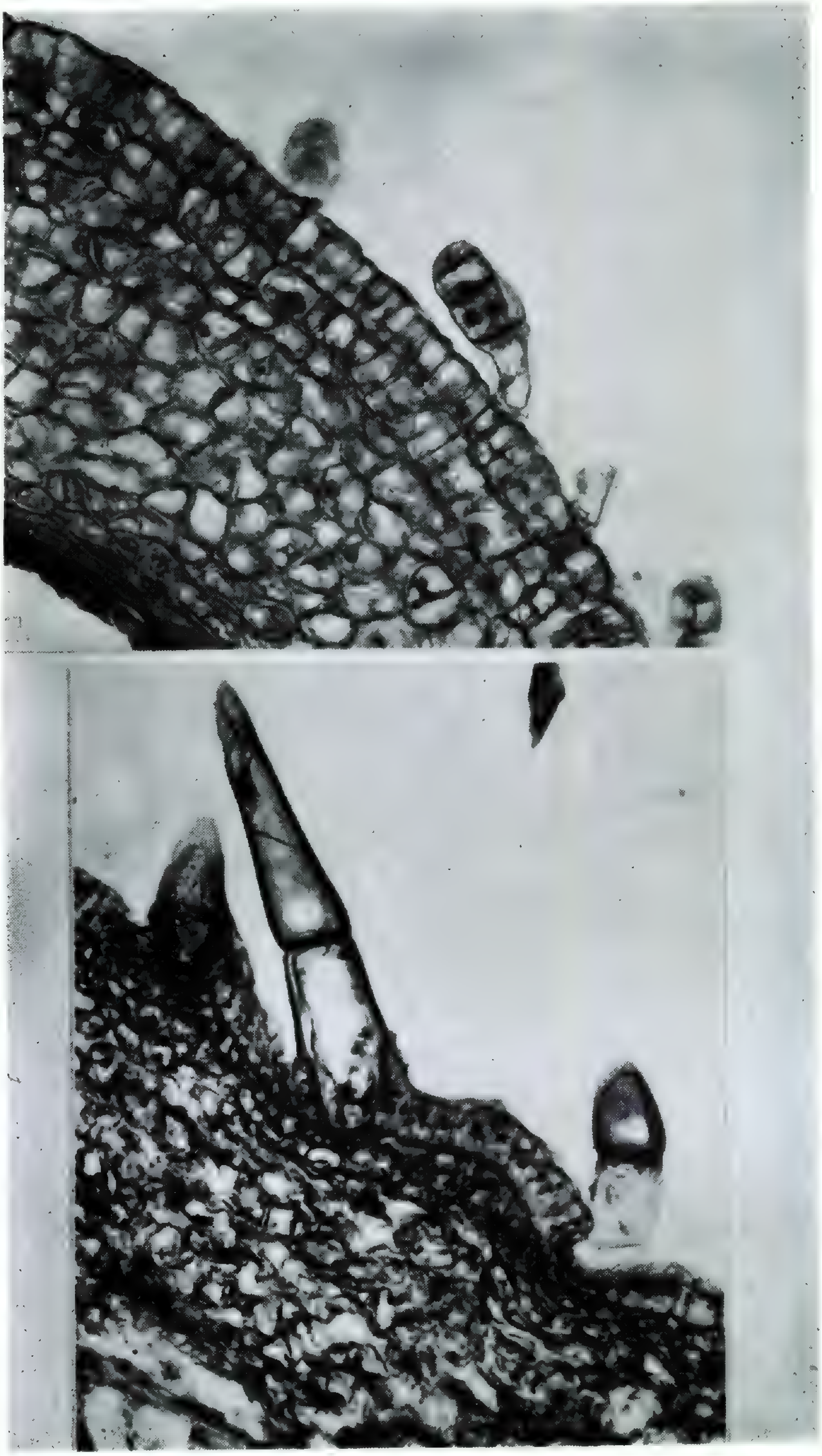

Fig. 21. Cross section of fruit wall of *Toxicodendron toxicarium*. Upper: Developing wall, showing emerging trichomes, × 90. Lower: Later stage of development than in A, showing mature exocarpal hairs, × 90.

Fig. 22. Longisection of nearly mature fruit of *Toxicodendron toxicarium*. Upper: Functional resin ducts, beginning of endocarp sclerification, elongating embryo, × 75. Lower: Tissues of seed coat and endocarp, × 190.

colored substance at maturity.[12] Wrinkled exocarp, often seen in herbarium material, is merely an indication that the fruits are not ripe; the wrinkling occurs due to differential shrinking in the drying process.

The endocarp is a triple-layered tissue, consisting of a single basal layer of small, thick-walled cells, and a double layer of smaller, isodiametric, very thick-walled cells. Perpendicular to this endocarp layer is a single layer of thinner-walled elongate seed coat cells. Entire fruits with shrunken calyces and disks attached constitute the functional disseminules, although overwintering fruits clinging to the pedicels often lose their exocarps before dispersal. References in the literature to "seed" characters are interpreted as references to the mesocarp and its contents. The endocarp may separate from the mesocarp to some extent in some taxa, but never from the testa.

CHROMOSOME NUMBERS

Chromosome numbers were determined from observations of pollen mother cells. *Toxicodendron* species flower for a relatively brief period each year; hence, it was not possible to collect cytological material for chromosome counts in most of the taxa in this group. Counts were made for *T. radicans* subsp. *negundo* (Fig. 23), *T. rydbergii*, and *T. toxicarium* (Fig. 24). In all taxa for which counts were available, meiosis appeared regular and the chromosome number was the same. This figure of $2n = 30$ agrees with published counts of $n = 15$ for *T. diversilobum* by Copeland and Doyel, coroborated by the work of Raven, Kyhos, and Hill (1965), and for *Rhus toxicodendron* by Grimm (1912). In the latter case, we have no way of knowing which taxon was under study; from the context of the article, it might have been *T. radicans* subsp. *radicans*. Because of the small size, relative uniformity in size

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[12]The fruit trichomes of *T. trichocarpum* are unique in the genus. Their bases anastomose all over the surface of the fruit and finally project outward as hollow, curved, bristly hairs.

Fig. 23. Meiotic chromosomes in anther of *Toxicodendron radicans* subsp. *negundo*, × 200.

of the chromosomes, and difficulty in differentiating the kinetochore, karyotype analyses were not undertaken. In one pair of chromosomes in *T. toxicarium*, however, there appear to be satellites.

Material of *Toxicodendron* used in cytological investigations: *Toxicodendron radicans* subsp. *negundo*, *Gabriele Mühling s.n.*, Michigan, Oakland County, 5 miles north of Farmington on 12-Mile Road between Halstead and Haggerty, 11 May 1959. *Toxicodendron rydbergii*, *Gillis* 5549, Michigan, Alger Co., T. 49N., R. 14W., SW 1/4 Sec. 7. Devil's Slides on high sand dune overlooking Lake Superior. 17 June 1964. *Toxicodendron toxicarium*, *Gillis* 4315, Florida, Alachua County, T. 9S., R. 19E., Sec. 13, 12 miles NW of Gainesville, San Felasco area. Turkeyoak-pine Woods. 6 April 1961.

SPECIMENS EXAMINED

In the citation of specimens, herbarium abbreviations in the fifth edition of "Index Herbariorum" (Lanjouw and Stafleu, 1964) have been used. Those herbaria which are not included in the Index have been assigned provisional abbreviations marked with a plus (+). The herbaria and

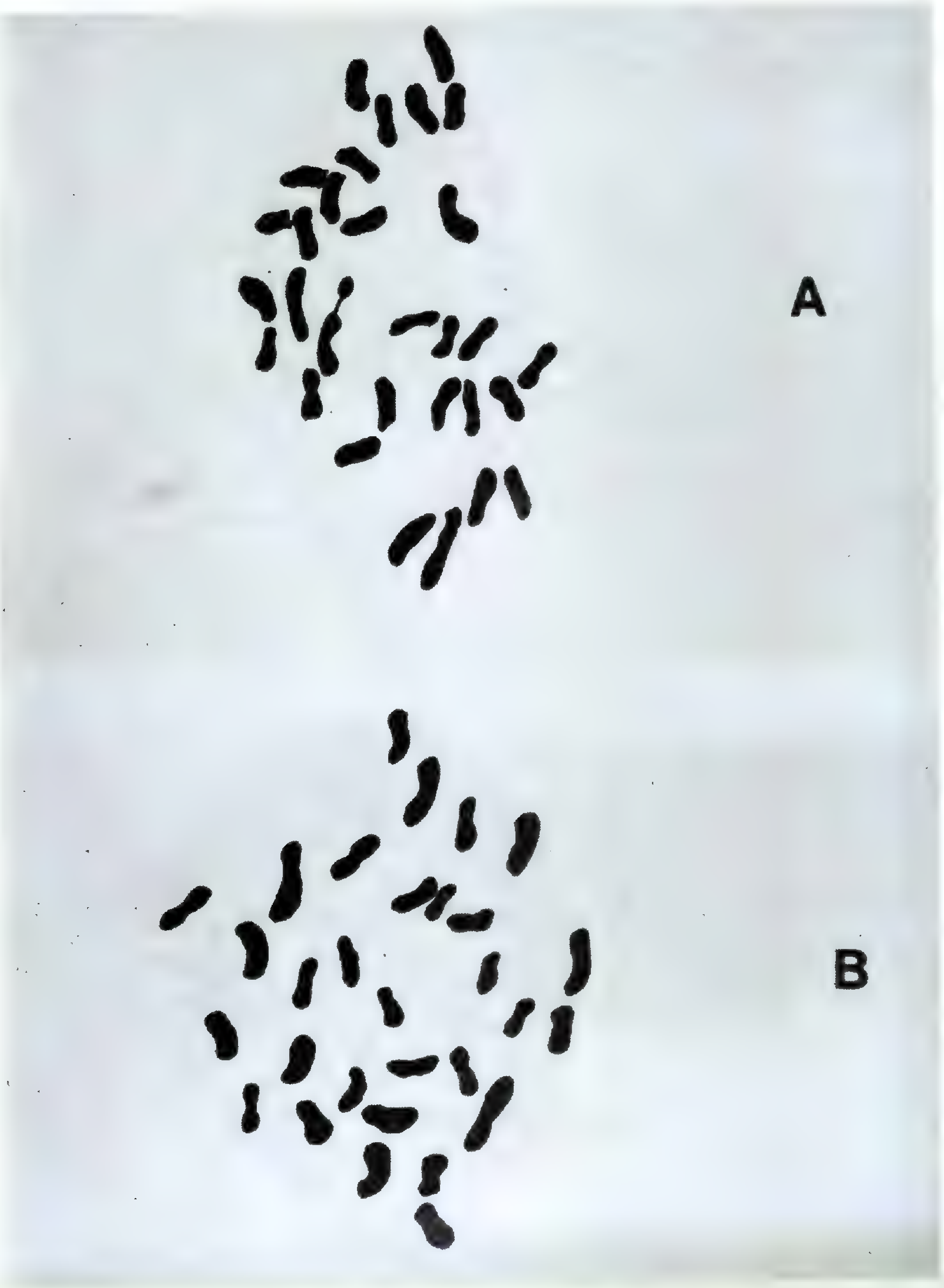

Fig. 24. Chromosomes of *Toxicodendron*. A, *T. toxicarium*, Alachua county, Florida, Gillis 4315. B, *T. rydbergii*, Alger county, Michigan, Gillis 5549.

their abbreviations are: Arnold Arboretum of Harvard University (A); University of Alberta (ALTA); Mohr Herbarium, Alabama Museum of Natural History (ALU); University of Arizona (ARIZ); Arizona State College (ASC); Cranbrook Institute of Science (BLH); British Museum (Natural History) (BM); Herbarium Bogoriense, Lembaga Biologi Nasional (BO); Brigham Young University (BRY); Central National Herbarium, Calcutta (CAL); Chrysler Herbarium, Rutgers University (CHRB); Plant Research Institute, Canada Dept. of Agriculture, Ottawa (DAO); Dayton Museum of Natural History (DMNH+); Dudley Herbarium, Stanford University (DS); Duke University (DUKE); Royal Botanic Garden, Edinburgh (E); Escuela Nacional de Ciencias Biologicas, Mexico City (ENCB+); Chicago Natural History Museum (F); Florida Agricultural Experiment Station (FLAS); Florida State University (FSU); Conservatoire et Jardin Botaniques, Geneva (G); University of Georgia (GA); Gray Herbarium of Harvard University (GH); University of Illinois (ILL); Herbarium, Kew (K); Kansas State University (KSC); Botanical Institute, Kiew, Ukranian S.S.R. (KW); Rijksherbarium, Leiden (L); Catholic University of America (LCU); Komarov Botanical Institute, Leningrad (LE); Linnaean Society (LINN); University of Michigan (MICH); Public Museum, City of Milwaukee (MIL); University of Minnesota (MIN); Missouri Botanical Garden (MO); Michigan State University (MSC); Universite de Montreal (MT); University of Notre Dame (ND); Greene Herbarium, University of Notre Dame (ND-G); North Dakota State University (NDA); New York Botanical Garden (NY); Botanisk Museum, Oslo (O); Oregon State University (OSC); Fielding Herbarium, Oxford University (OXF); Muséum National d'Histoire Naturelle, Paris (P); University of Pennsylvania (PENN); Philadelphia Academy of Natural Sciences (PH); Rocky Mountain Herbarium, University of Wyoming (RM); Hokkaido University (SAP); South Dakota State College (SDC); University of South Dakota (SDU); Botanic Gardens, Singapore (SING); Southern Methodist University (SMU); Sul Ross

State College (SRSC); National Taiwan University (TAI); University of Texas (TEX); Botanical Institute, Tokyo University (TI); Botanical Museum, Utrecht (U); University of California, Berkeley (UC); United States National Museum (US); University of Manitoba (WIN); University of Wisconsin (WIS); and Wayne State University (WUD).

(To be continued)

DIPLACRUM AFRICANUM NEWLY FOUND IN TROPICAL AMERICA: A small tropical sedge, *Diplacrum africanum* C. B. Clarke, previously known as an endemic to Africa, has been collected from southern Suriname near the Brazilian border. The collection is: SURINAME. Sipaliwini savanna area on Brazilian frontier, 1.5 km NNW of 4-Gebroeders Mountains, 300 m alt., on plain in wet valley near a Mauritia-swamp, ON 152, *F. H. F. Oldenburger, R. Norde & J. P. Schulz*, Sept. 1968 (BBS, NY, U). This particular specimen was found growing in sandy soil with an impeded water table through the rock pavement at a depth of ca. 50 cm. Among the associated plants from the same locality were *Philodice hoffmanseggii, Syngonanthus glandulosus, S. gracilis* var. *koernickeanus, Bacopa monierioides, Centunculus pentander, Polygala paludosa, Utricularia adpressa* and *Eleocharis nana*.

Diplacrum africanum belongs to the section *Sphaeropus* of the genus bcause of its fruits, which fall off apart from the subtending glumes, and the spongy thickened receptacle below the upper glumes. Such thickenings are presumed to be formed by the adnation of abortive staminate spikelets to the base of the reduced glumes, and are seen also in a few species of the genus *Becquerelia*, showing the close taxonomic affinity between *Diplacrum* and *Becquerelia* (cf. T. Koyama, in Mem. N. Y. Bot. Gard. 17: 23-79. 1967).

Diplacrum section *Sphaeropus* involving two other Asiatic species has hitherto been noted from tropical Africa

and Malaysia, and now has a range extension into northern South America. The previously known range of *D. africanum* covers Upper Guinea, Nile Land and Madagascar. Other cyperaceous taxa that exhibit similar Afro-American phytogeographic links include *Diplacrum capitatum* (=*longifolium*), *Scirpus cubensis, Rhynchospora cyperoides, Mapania monosperma/maguireana, Mapania* sect. *Mapania* (*M. sylvatica* & *assimilis/gabonica*), *Hypolytrum lancifolium/stemonifolium* and *Afrotrilepis/Trilepis.*

TETSUO KOYAMA
NEW YORK BOTANICAL GARDEN
BRONX, NEW YORK

FEDDO H. F. OLDENBURGER
NETHERLANDS FOUNDATION FOR
THE ADVANCEMENT OF TROPICAL RESEARCH (WOTRO)
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Volume 73, No. 793, including pages 1-160, was issued March 31, 1971.

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JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Conducted and published for the Club, by

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Vol. 73 June, 1971 No. 794

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The New England Botanical Club, Inc.

Botanical Museum, Oxford St., Cambridge, Mass. 02138

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LEXINGTON, MASSACHUSETTS

Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 73 June, 1971 No. 794

THE SYSTEMATICS AND ECOLOGY OF POISON-IVY AND THE POISON-OAKS (TOXICODENDRON, ANACARDIACEAE)[1]

WILLIAM T. GILLIS

(Continued from page 159)

TAXONOMIC TREATMENT

TOXICODENDRON Miller

Toxicodendron Tournefort, Inst. Rei Herb., p. 610. 1700; Miller, Gard. Dict., Abr. ed. 4. 1754, non *Toxicodendron* = *Toxicodendrum* Thunb. in Kongl. Vetensk. Acad. Nya Handl. 7: 188. 1796. (= *Hynaenanche* Lam., Euphorbiaceae), nec *Toxicodendrum* J. Gaertner in Fruct. 1: 207. 1788 (= *Allophylus* L. or *Schmidelia* L., Sapindaceae).

Rhus L., Sp. Pl. 1: 265. 1753, in part as to species 4, 6, and 7.

Vernix Adanson, Fam. Pl. 2: 342. 1763.

Rhus-Toxicodendron Marshall, Arbust. Am., p. 130. 1785.

Pocophorum Necker, Elem. Bot. 2: 226. 1790.

Philostemon Raf., Fl. Ludoviciana, p. 107. 1817; Steudel, Nom. Bot. ed. 2: vol. 2., p. 320. 1841 as *Philostemum*.

Deciduous dioecious trees, shrubs, or woody vines with poisonous effluvium. Leaves alternate, palmately ternate or imparipinnate, estipulate, thin, glabrous to tomentose on the lower surface, glabrous to sericeous on the upper surface; leaflets opposite except for the terminal one. Flowers in axillary, lateral, thyrsoid panicles or racemes, ultimate clusters determinate, of 3 or 4 flowers; bracts of the inflorescence lanceolate, deciduous; fruiting inflorescence

usually pendent, but occasionally erect by lignification of the rachis. Sepals 5, persistent, imbricate in the bud, united at base. Petals 5, ascending, veined, glabrous, imbricate in bud, ovate, usually with reflexed tips, smaller in female flowers than in male. Ovary 1-celled by abortion, sessile or partially buried in the hypogynous disk; style terminal, stigma 3-parted, turning black with age; ovule raised on an elongate ascendent basal funicle. Drupes subglobular or laterally flattened, 2.5-7 mm broad, 1.5-5 mm long, whitish, cream, yellow, to dun-colored, glabrous or pubescent with simple, non-glandular hairs, less than 1.5 mm long, the bony endocarp and mesocarp adhering; mesocarp waxy, striate with black resin canals; exocarp brittle, papery, separating from the mesocarp at maturity; remnant of the 5-lobed disk becoming chartaceous. Stones bony, often with a few ribbon-like longitudinal ridges, endocarp fused to testa; endosperm absent; embryo large, generally transverse with flat foliaceous cotyledons; hypocotyl ± elongate, incurved upwards toward the hilum. Stamens 5, haplostemonous, inserted below a lobed, annular, patellior, cupuliform, intrastaminal, nectiferous disk, reduced in female flowers; anthers oblong, dorsifixed, usually shorter than the ± subulate filaments; dehiscence longitudinal, introrse. Pollen tricolpate, finely reticulate, ellipsoidal, with tapering transverse furrows, endexine thickened internally at the edge of the colpus forming a rib; mean length 26.6μ, mean width 23μ. Vessels not clustered in the late wood; resin ducts absent in the xylem rays; septate xylem fibers present; with solid, white. Root ribrous; root hairs dark brown. North America to northern South America, and eastern Asia.

Type species; *Toxicodendron toxicarium* (Salisb.) Gillis (*Rhus toxicodendron* L., Sp. Pl. 1: 265. 1753, lectotype of Barkley, 1937).[13]

[13]Barkley (1937) named *Rhus toxicodendron* L. as lectotype species of sect. *Eutoxicodendron* (= sect. *Toxicodendron*) and equated it with *Toxicodendron radicans*. However, it is now clear that *Rhus toxicodendron* of Linnaeus = *T. toxicarium*, and therefore this is the correct name for the lectotype species of the genus.

KEY TO SECTIONS, SPECIES, AND SUBSPECIES OF TOXICODENDRON

a. Large shrub or tree, clonal, but without long stolons; anthers conspicuously exserted, filaments filiform .... Section Venenata (not treated herein)

a. Vine, sub-shrub, or shrub with long stolons; anthers included, filaments subulate at the base b.

b. Leaves simple (Section Simplicifolia) .... 1. *T. borneense*

b. Leaves compound c. (Section Toxicodendron)

c. Leaflets 5 - 9 .... 2. *T. nodosum*

c. Leaflets 3 d.

d. Fruits glabrous (or with only occasional hairs); leaflets coarsely toothed, 1-lobed, or entire; if entire, then tufts of hairs concentrated in vein axils on lower surface absent e.

e. Leaflets with lobed or deeply cut margins .... 4h. *T. radicans ssp. verrucosum*

e. Leaflets with entire, undulate, notched, or serrate margins f.

f. Leaflets glabrous to scattered-strigose on the lower surface, or with pubescence confined to the veins, not velvety to the touch; glabrous or with sparse pubescence on the upper surface; pubescence, if any, appressed g.

g. Most leaves made up of entire or subentire leaflets .... 4g. *T. radicans* ssp. *divaricatum*

g. Most leaves made up of notched or serrate leaflets h.

h. Leaflets suborbicular or broadly ovate; petiole completely glabrous; plant subshrub or shrub .... 5. *T. rydbergii*

h. Leaflets ovate or lanceolate; petiole puberulent to densely pubescent; plant shrub or vine .... 4f. *T. radicans* ssp. *negundo*

f. Leaflets densely pilose to velutinous on lower surface, velvety to the touch; pubescence on the upper surface; pubescence erect i.

i. Leaflets serrate; terminal leaflet broadly ovate .... 4d. *T. radicans* ssp. *pubens*

i. Leaflets entire or subentire; terminal leaflet elliptic or lanceolate .... 4e. *T. radicans* ssp. *barkleyi*

d. Fruits pubescent or papillose; leaflets entire, undulate, or round-lobed; if toothed, then tufts of hairs in vein axils on lower leaflet surface present j.

j. Leaflets mostly obtuse or rounded at apex; fruits setose or minutely puberulent; tufts of hairs absent from vein axils on lower leaflet surface k.

k. Leaves glabrous to glabrate .... 3. *T. diversilobum*

k. Leaves pubescent l.

l. Leaflets deeply incised; leaflet base rounded .... 4i. *T. radicans* ssp. *eximium*

l. Leaflets undulate or lobed; leaflet base cuneate .... 6. *T. toxicarium*

j. Leaflets acute or acuminate; fruits puberulent, hispid or scabrous; tufts of hairs present in vein axils on lower leaflet surface m.

m. Widest part of terminal leaflet blade below centre; tufts of hairs in vein axils usually not red-brown; terminal leaflet blade 2.5-14 cm. long; fruits globose, 3-5 mm. broad; terminal leaflet obtuse or truncate .... 4a. *T. radicans* ssp. *radicans*

m. Widest part of terminal leaflet blade at or above centre; tufts of hairs in vein axils usually red-brown; terminal leaflet 6-20 cm. long; fruits flattened, often obliquely deltoid, 5-6 mm. broad; terminal leaflet attenuate or cuneate n.

n. Fruits short hairy or papillose only; terminal leaflet 1.2-1.7 times as long as broad, cuneate .. .. 4b. *T. radicans* ssp. *orientale*

n. Fruits hispid with hairs nearly 1 mm. long; terminal leaflet nearly twice as long as broad, attenuate .... 4c. *T. radicans* ssp. *hispidum*

Toxicodendron section **Simplicifolia** Gillis, sect. nov.

Vites lignosae deciduae; folia simplicia, subcoriacea; fructus elevatus super vestigium receptaculi et disci.

Deciduous woody vines; leaves simple, subcoriaceous; fruit raised from remnant of receptacle and disk. Northern Borneo (Sabah). Type species: *Toxicodendron borneense* (Stapf) Gillis.

1. **Toxicodendron borneense** (Stapf) Gillis, comb. nov. Fig. 25.

Fig. 25. *Toxicodendron borneense.* Right, above: Holotype of *Rhus borneensis* Stapf, *Haviland* 1198 (Male). Right, below: *Haviland* 1224 (female). Left: Fruiting specimen, *Meijer.*

Rhus borneensis, Stapf in Trans. Linn. Soc. London Bot. 4: 142. 1894. Type: *G. D. Haviland* 1198, 6000 ft. on Mt. Kinabalu, Sabah, 19 March 1892 (K) male flowering specimen.

Scandent shrub; branches slender, brown, often bearing prominent lenticels. Leaves simple, subcoriaceous, elliptic to oblanceolate, short petiolate, entire with revolute margins, with 14-22 pairs of ± prominent veins; glabrous, with acuminate to mucronate tips, base attenuate; blade 6-16 cm long, 2.5-6.5 cm broad. Inflorescence a lateral paniculate

thyrse, 6-14 cm long, longer in female than in male, generally in verticillate clusters with leaves above and below; flowers clustered often in threes on short, minutely bracteoluate pedicels; bracts lanceolate, 1 mm long, 0.2 mm wide, glabrate, gradually tapering to a blunt tip, narrower in female than in male; corolla lobes oblong to oblanceolate, 2.0-2.8 mm long, 1.0-1.5 mm broad, narrower in female than in male, blunt; fertile anthers 1.2 mm long, broadly ovate, filaments 0.5 mm long; in female sterile anthers 0.5 mm long, subulate. Fruiting inflorescence glabrous, erect; fruit obliquely globose-reniform, laterally flattened, 5.5-7 mm broad, 5-6 mm deep at its widest point (through the stigmatic region), glabrous, with mesocarp striate in a white, waxy matrix; fruit raised from remnant of receptacle and disk.

Specimens examined: **Malaysia:** Sabah; Mt. Kinabalu, 6000 ft., *Haviland* 1198, (K); 6600 ft., *Haviland* 1224, (K); Kamberanga, 7040 ft., *Griswold* 118, (A); Gunong Alab, Tambunan, 4000 - 5000 ft. *Meijer* (K, SAN).

Distribution: Province of Sabah (Borneo), Malaysia. Fig. 26.

Toxicodendron borneense is the rarest of the species in the poison-ivy complex. It has been collected only four times. On one occasion, the collector noted that his collection came from a fresh branch found on the ground, no parent plant having been discovered from which it may have come. The range of variation in the species is therefore unknown. Although its type locality is Mt. Kinabalu in the state of Sabah in northern Borneo, a mountain which has been visited by several plant-collecting expeditions, *T. borneense* has been found there only twice.

This species shares with all other *Toxicodendron* species the property of possessing resins which darken with age (presumably poisonous) in addition to their diagnostic fruit and flowers characteristics. It differs markedly in having simple leaves and verticillate inflorescences. The fruits appear to be raised on a remnant of the receptacle and disk, unlike other members of the genus. Because of

Fig. 26. *Distribution of Toxicodendron borneense* and *T. nodosum.*

these unique characters which set *T. borneense* apart from the rest of the genus, a new section of the genus has been erected for it.

Toxicodendron sect. **Toxicodendron**

Eutoxicodendron Schneider, Illustr. Handb. Laubholzk. 2: 149. 1907.

Toxicodendron Robinson & Fernald, Gray's New Manual, p. 552. 1908, as subgenus.

Sumac DC., Prodr. 2: 67. 1825, as sect. in part.

Deciduous woody vines or small shrubs with comparatively slender branches and tendency to proliferate extensive rhizomes. Flowers in small, axillary thyrses; stamens with short subulate filaments and elongate, included anthers; fruits usually pendent. Leaves palmately trifoliolate or pinnately penta- or septi-foliolate, alternate, with phyllotaxy 3/8. North America from Canada to western Guate-

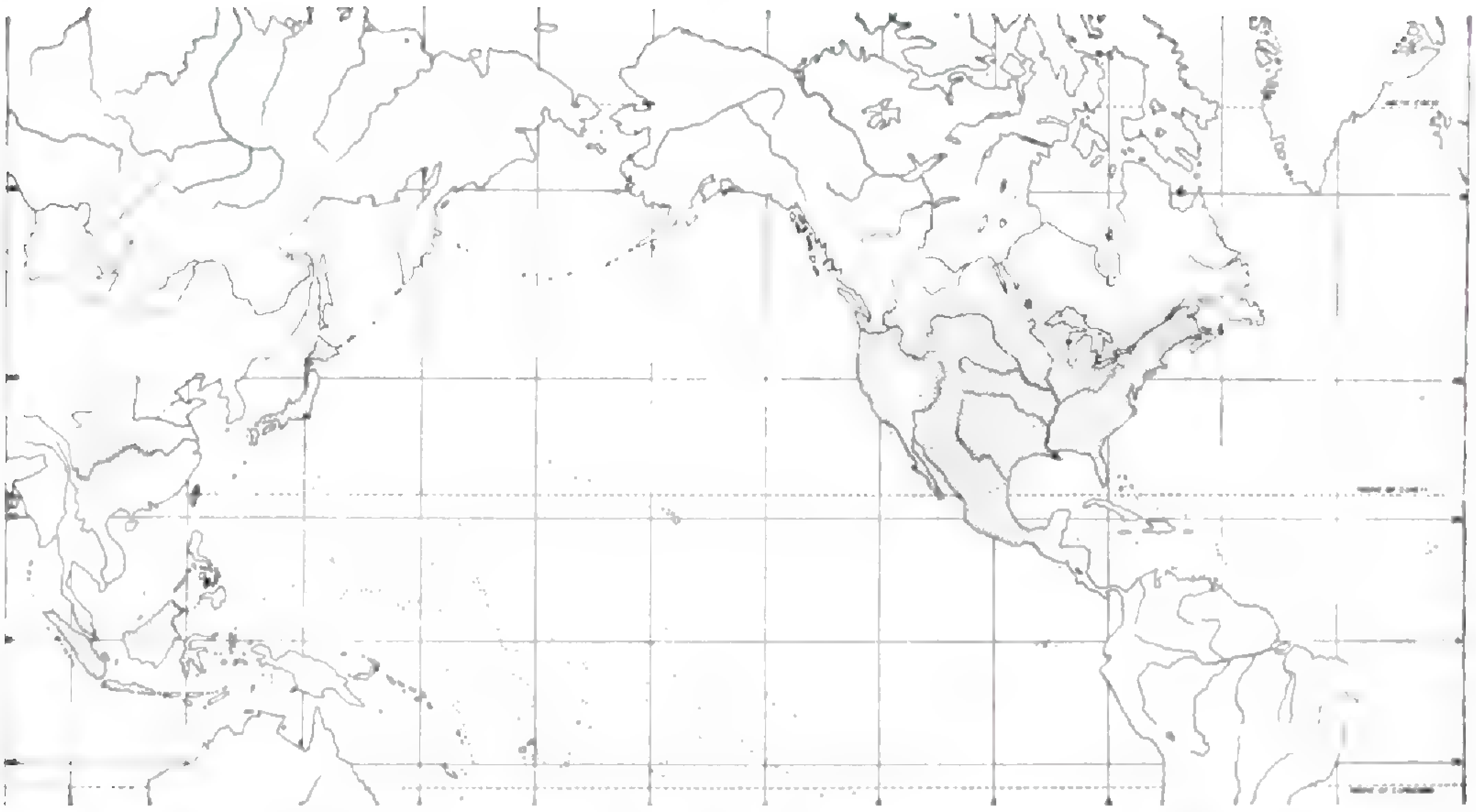

Fig. 27. Distribution of the genus *Toxicodendron* sect *Toxicodendron.*

mala; Asia: Japan, China, Taiwan, Malaysia, Indonesia, and U.S.S.R.: Sakhalin and Kurile Islands. Fig. 27.

2. **Toxicodendron nodosum** (Blume) Gillis, comb. nov. Fig. 28.

Rhus nodosa Blume, Bijdragen tot de Flora van Nederlandisch Indie, 17: 1164. 1826. Type: Java, collector unknown (L, holotype).

Rhus perakensis Scortechini ex King in J. Asiat. Soc. Bengal Pt. 2 Nat. Hist. 65: 500. 1896. Type: *Scortechini* 1668, Perak, Malaya (CAL- 98286, holotype).

Scandent shrub up to 15 meters long with occasional roots; branches slender, red-brown, often bearing prominent lenticels. Leaves imparipinnate; leaflets 5-7 (-9), elliptic-lanceolate to oblong with 14-20 pairs of veins which are ± prominent beneath, entire, completely glabrous or with occasional hairs, with long acuminate tips, rounded or truncate to obtuse or attenuate at the base, short petiolulate (petiolules less than 1 cm) or subsessile except for the terminal leaflet; blade 5-15 cm long, 2.5-5.5 cm

Fig. 28. *Toxicodendron nodosum.* Type of *Rhus nodosa* Blume, Java.

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broad, generally longer in Bornean than Mayalan or Javan populations; petiole 15-30 cm long, glabrous; petiolule 2-4 mm long, glabrous; terminal petiolule 7-15 mm long, glabrous or exceedingly finely puberulent. Inflorescence a lateral or subterminal thyrse, 15-40 cm long; flowers abundant, tightly clustered on short, minutely bracteolulate, glabrate or puberulent pedicels; bracts oblanceolate, 0.2-0.3 mm long and broad, glabrate, deciduous; calyx 0.5-1.7 mm long, 0.5-1.0 mm broad, narrower in female than in male, glabrous; fertile anthers 1.2 mm long, broadly ovate; filaments linear-subulate, 0.8-1.5 mm long, in female sterile anthers 0.4 mm long, subulate, filament 1.5 mm, pubescent; pollen 20.8-28.5μ long, 17.5-22.0μ broad. Fruiting inflorescence puberulent or glabrous, pendent; fruit obliquely globose-reniform, 5.0-8.0 mm across, 3.0-6.0 mm broad, glabrous with mesocarp striate in white waxy matrix; exocarp dun-colored. Buds stalked, naked, mucronate, brown, covered with brown pubescence.

Distribution: Indonesia and Malaysia. At elevations from sea level to 1500 meters growing in shallow soil on limestone, apparently rare. Fl. Aug.-Dec.; fr. Oct.-Mar. Local name: "jahor" (Burkhill, 1935). Fig. 27.

Specimens examined: **Indonesia:** CELEBES; Makassar, collector unknown (BO). JAVA: Batavia Tijanten, *Backer* 25958 (BO); Nirmala, *Backer* 10622 (BO); G. Batoe, *Backer* 25802 (BO); Josoredja en Dara, Pekalongan, *Backer* 16275 (BO); Tjidadap, Bangas, 1000 meters, *Bakhuizen van den Brink* 875 (L); Preanger Regentschappen, Geger Bentang, *Lapün, s.n.* (BO); Preanger G. Karang, *Bakhuizen van den Brink* 833 (BO); locality and collector unknown (Type) (L); SUMATRA: Batang Baroes, *Tegsmain, s.n.* (BO); Sekintjau Belirang, 1400 m., *Rappard* 79 (BO).

Malaysia: PERAK: Larut, *King's collector* 6807 (BM, CAL, L); locality unknown, *Scortechini* 1668 (CAL); Tupai, *Wray* 3095 (CAL, SING); Thaipeng, *Wray* 3054 (SING). SARAWAK: Bau, *Haviland* 1965 (CAL); Bau, *Purseglove* 4440 (A, L, SING); Kuching, *Haviland & Hose* 3366 E (BO, L); Mt. Buan, *Haviland* 1962 (SING); Tambusan, HM 12310 (SING); Mt. Dulit near Long Kapa, 400 m., *Richards* 1468 (A, L); Stetapok F. R., 4 miles south of Kuching, limestone hills, *Anderson* S.25131 (MSC).

Toxicodendron nodosum is described (as *Rhus perakensis*) by Corner (1940) as being like one of the "poison ivies of North America." Like poison-ivy, it is a vine or climber; unlike poison-ivy, it has five to seven leaflets. Its inflorescences are longer than those of poison-ivy. As in the case of other members of this complex, *T. nodosum* has been referred to the genus *Rhus* by various authors. It shares with all other Toxicodendrons, however, smaller pollen than that of *Rhus* species, toxic effluvium, absence of glandular hairs, buff to tan exocarps, striate mesocarps, and chiefly axillary inflorescences. Some flower clusters occupy a sub-terminal position, but in all specimens that have been examined, there is a vegetative shoot continuing beyond the inflorescences, continuing terminal growth. Because of its scandent habit, anther size, shape, and position, *T. nodosum* has been placed in section *Toxicodendron* of the genus.

Collections made in former Dutch possessions have been called *Rhus nodosa*, while those collected in regions of the British Commonwealth more likely have been named *R. perakensis*. On the basis of herbarium material examined, it is not possible to distinguish between these two taxa.

This is a rarely collected plant, its rarity probably due more to inaccessibility than to actual lack of abundance. It is found in the mountainous areas of northern Perak in the Malay Peninsula, on limestone ridges near Bau and Kuching in the state of Sarawak in Borneo, and scattered throughout Sumatra, Java, and Celebes. Presumably it grows in Indonesian Borneo, but no collections from this region are known. It has been collected only six times since 1920. Label data on herbarium specimens are generally scanty, so that it would not be possible to return to the exact site of a previous collection.

Recent collections were desired to study fresh seeds inasmuch as some important diagnostic characters are found in the fruits of this genus. The *Purseglove* 4440 specimen indicates that the seeds were "red, drying buff," yet the fresh seeds suggest that the exocarps could hardly ever have been red. They certainly are buff, and show the plant to be a *Toxicodendron*. (Acknowledgement is made of Mr.

J. A. R. Anderson, Conservator of Forests in Kuching, who kindly sent fresh material of this species for study.)

Like many other *Toxicondendron* species, *T. nodosum* seems to occur chiefly in limey areas. It is generally found in shallow, rocky soils in open jungle, climbing trees up to 15 meters. Its ecology is incompletely known due to the paucity of collections and collection data, particularly in recent years. Backer and Bakhuizen Van Den Brink (1965) suggest that the plant in Java occupies the wetter sites (up to only three dry months per year, where rainfall greater than 100 mm per month = "wet") at altitudes of 900-1200 m. They, in fact, label it as an "everwet climate" indicator. Flowering season for the plant seems to vary from July to December, possibly just prior to onset of monsoon seasons. It appears not to be a heavy seeder.

Backer and Van Den Brink (*ibid.*) further describe the petiolules as being winged. From all specimens I have examined, I would describe this condition as the attenuate nature of the terminal leaflet base, rather than a true "winged" nature of the rachis as in *Rhus javanica* and *R. copallina.* In the latter, the winged condition extends from the terminal leaflet to the base of the lowest leaflet; in *Toxicodendron nodosum*, it is merely restricted to the base of the terminal leaflet.

From a plant grown from seed in the laboratory, one can see that the young seedling has simple leaves for an appreciable period of time before any compound leaves appear, well after the stem has begun to lignify. The first compound leaves appeared on one such laboratory-grown plant only after 11 simple leaves were produced. Throughout this time, the cotyledons remained on the plant and remained green.

3. **Toxicodendron diversilobum** (T. & G.) Greene, Leafl. Bot. Observ. Crit. 1: 119. 1905. Figs, 29, 30.

Rhus diversiloba T. & G., Fl. N. Am. 1: 218. 1838. *Rhus toxicodendron* subsp. *diversiloba* (T. & G.) Engler in DC.,

Fig. 29. *Toxicodendron diversilobum.* Type of *Rhus lobata* Hook., *Douglas.*

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Fig. 30. *Toxicodendron diversilobum.* Type of *T. oxycarpum* Greene, *J. Ball.*

Monog. Phaner. 4: 395. 1883. *Rhus toxicodendron* var. *diversiloba* (T. & G.) Brandegee, Zoe 2: 345. 1892. *Toxicodendron radicans* subsp. *diversiloba* (T. & G.) Thorne, Aliso 6: 28. 1967 (corrected to *T. radicans* subsp. *diversilobum*, ibid. p. 86.). Type: *Nuttall, s.n.* "California," (NY, holotype).

Rhus lobata Hook., Fl. Bor. Am., p. 127. 1830, non Poiret, Ency. Meth. Suppl. 5: 264. 1804. *Rhus varielobata* Steudel, Nom. Bot. 2: 452. 1841 (nomen nudum). Type: *Douglas, s.n.* British Columbia, Fort Vancouver, June, common on the outskirts of woods in dry soils (K, holotype).

Toxicodendron comarophyllum Greene, Leafl. Bot. Observ. Crit. 1: 120. 1905. Type: *Palmer* 45, California, San Diego Co., Tighe's near San Diego, 1875. (US-19802, holotype; F-302931, isotype; MO-1773737, possible isotype).

Toxicodendron oxycarpum Greene, Leafl. Bot. Observ. Crit. 1: 121. 1905. Type: *J. Ball, s.n.*, California, Santa Cruz Co., Redwood Forest, Santa Cruz, 10 July 1894. (US-292229, holotype).

Toxicodendron isophyllum Greene, Leafl. Bot. Observ. Crit. 1: 121. 1905. Type: *John B. Leiburg* 3117, California, Riverside Co., river banks near San Jacinto, 600 meters elevation, 9 March 1893. (US-342019, holotype).

Toxicodendron dryophilum Greene, Leafl. Bot. Observ. Crit. 1: 121. 1905. *Rhus diversiloba* f. *radicans* McNair, Publ. Field Mus. Nat. Hist. 225. Vol. 4: 61. 1925. Type: *Mrs. R. M. Austin, s.n.*, Butte Co., climbing oak trees in Little Chico Canyon, May 1896. (ND-G-22098, holotype; MO-1773736, US-28527, isotypes).

Toxicodendron vaccarum Greene, Leafl. Bot. Observ. Crit. 1: 122. 1905. Type: *M. S. Baker and Frank Nutting, s.n.*, 23 May 1894. As *T. vacicarum* McNair, in syn., Publ., Field Mus. Nat. Hist. 225. Vol. 4: 59. 1925. (ND-G, holotype; MO-1114683, photograph of type).

Rhus diversiloba f. *quinquifolia* McNair, Bull. Torrey Bot. Club 63: 476. 1936. Type: *A. Wood s.n.*, 1866 (NY, lectotype).

Vine, shrub, or rarely tree, with slender, glabrous to puberulent branches, usually with brown aerial roots; rhi-

zome creeping; leaves crowded on branches. Bark gray-brown to red-brown on new wood, becoming gray on older wood; leaf scars V- or U-shaped with 6-10 bundle scars; lenticels usually conspicuous. Buds stalked, naked, mucronate, brown, covered with a brown woolly pubescence. Autumn coloration scarlet to red-violet. Leaflets 3, occasionally 5 (-11), ovate, oblong, or suborbicular, entire, undulate, crenate-dentate or bluntly lobed; apex obtuse or rounded; base rounded, truncate, or subcuneate; lateral leaflets mostly inequilateral, 1.0-7.0 cm long, 1.0-6.0 cm broad; short petiolulate or subsessile; terminal leaflet 0.8-13.0 cm long, 0.3-8.0 cm wide, petiole 1.0-10.0 cm long; terminal petiolule 0.1-2.6 cm long; leaflets attached in palmate fashion when trifoliolate, pinnate when more than 3 leaflets; glabrous above, occasionally with a line of minute, curly hairs along the midrib, subpilose below or with trichomes restricted to appressed hairs on major veins. Leaves often mottled when dry. Inflorescences lateral paniculate thyrses up to 1 dm long; pedicels 2.0-8.0 mm long; bracts oblanceolate, 1 mm long, 0.3 mm wide, glabrate, ciliate, deciduous; sepals 5, yellow-green, deltoid-ovate, 1 mm long, 0.5 mm broad; filaments linear-subulate, 1.0-1.8 mm long. Drupe cream-colored, globose-reniform, sometimes obliquely deltoid, sometimes laterally flattened, 4.5-7.5 mm across, 1.5-5.5 mm broad with densely setulose exocarp becoming chartaceous upon ripening and readily separating from the mesocarp; mesocarp black striate in white, waxy matrix; endocarp dun-colored, bony.

Distribution: Northern Baja California, Western California, Oregon, and Washington, Vancouver Island, British Columbia. Common name: Western poison-oak. Fig. 31.

REPRESENTATIVE SPECIMENS

UNITED STATES. **California.** ALAMEDA CO.: Berkeley, *Greene, s.n.* (ND-G); Oakland, *Drew, s.n.* (F). AMADOR CO.: locality not cited, *Hansen, s.n.* (MO, ND-G, US); Ione, *Eastwood* 10153 (A). BUTTE CO.: Little Chico Creek, *Austin, s.n.* ND-G, MO, US); Big Chico Creek canyon, *Heller* 11211 (A, F, GH, MO, MIN, NY, OSC, ND-G, US); east of Chico, Stilson Canyon, *Heller* 12321 (A, F, MO, NY, OSC, US, WIS); Oroville, *Heller* 10787 (A, F, GH, MO, NY, US). Chico, *Palmer* 2060 (NY).

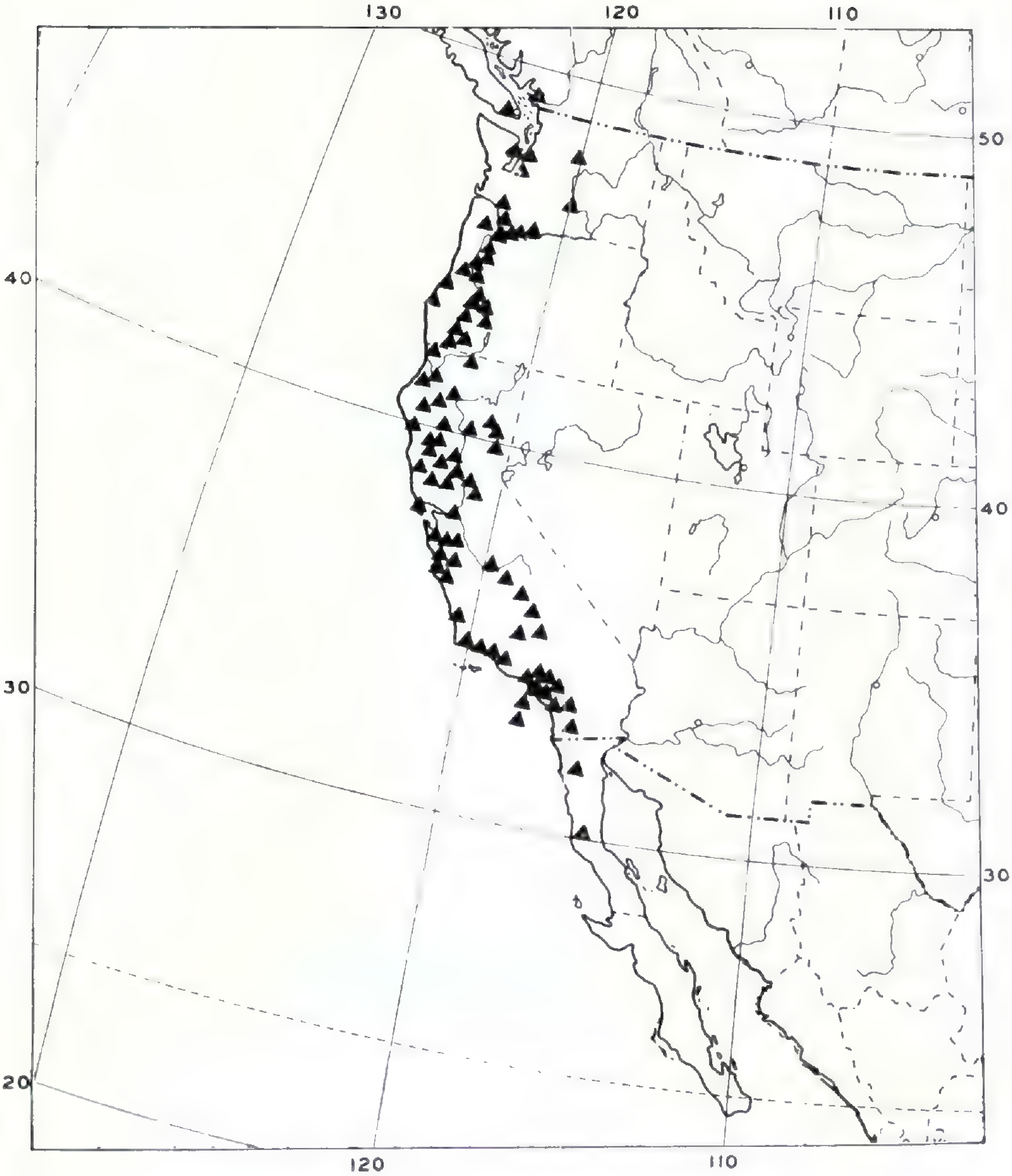

Fig. 31. Distribution of *Toxicodendron diversilobum*.

CALAVERAS CO.: Angels Creek, *Eastwood* 11622 (A); Calaveras River, *Gibbes, s.n.* (NY). COLUSA CO.: mountain slopes in chapparral, *Gillis* 4849 (MSC); Colusa, *Eastwood* 10236 (A). CONTRA COSTA CO.: Mt. Diablo, *Brewer* 1068 (GH); Clayton, *Brewer* 1068 (US); DEL-NORTE CO.: Gasquet, *Parks & Tracy* 11188 (GH, US). EL DORADO CO.: east slope of densely vegetated stream bank, 4 miles NE of Aulrun, *Holloway* 47 (ARIZ). GLENN CO.: Stonyford along Stonyford Creek, *Weston, s.n.* (MSC); Elk Creek, near Stonyford, *Gillis* 4865 (MSC). HUMBOLDT CO.: Humboldt State Park, *Weston, s.n.* (MSC); Willow Creek, *Tracy* 18404 (MO, US); Blacksburg, *Tracy* 15301 (GH, NY). JACKSON CO.: Walker Creek, *Applegate* 2339 (US). KERN CO.: Fort

Tejon, *DeVasey* 19 (GH, NY, US); Havilah, *Grinnell* 362 (US); Caliente Canyon, *Ziqmond* 138 (F). LAKE CO.: 1.1 miles east of Middletown on road to Lower Lake, serpentine soil, *Morley* 585 (CAL, MSC); Mt. Konocti, *Blankinship, s.n.* (MO); Middle Creek, 6 miles south of Elk Mountain, between Lake Pilsbury and Lower Lake, *Everett & Balls* 20355 (NY, RM). LOS ANGELES CO.: Santa Catalina Island, *Millspaugh* 4734 (F), Avalon Canyon, *Smith* 5069 (F, US); Hamilton Canyon, *Fosberg* 54301 (A, F, MO, NY, US); Swain's Canyon, *Nuttall* 622 (F, US); Claremont, *Whited* 885 (ND); Topango Canyon, Santa Monica Mountains, *Epling & Ellison, s.n.* (OSC); Pasadena, *Jones* 3206 (A, MSC, MO, NY, US); Mandeville Canyon, Santa Monica Mts., *Epling, s.n.* (A, MO, OSC, US); Temescal Canyon, Pacific Palisades, *Hastings, s.n.* (NY); Bouquet Canyon, San Gabriel Mts., *Templeton* 7702 (NY); Eagle Rock Valley, *Smith* 4904 (F, US). MADERO CO.: North Fork, *Griffiths* 4531 (NO, US). MARIN CO.: Taylor State Park, *Gillis* 4832 (MSC); Reyes Point, *Gillis* 4795 (MSC); 6 miles SE of Lagunitas, west of Fairfax, *Gillis* 4797 (MSC); Rose Valley, *Eastwood, s.n.* (A); Tamalpais, *Kountze* 23146 (NY); Mill Valley, *Eastwood* 6885 (A, NY). MARIPOSA CO.: Mariposa, *Congdon, s.n.* (MIN); Sherlocks, *Congdon, s.n.* (MIN). MENDOCINO CO.: Mendocino, *Brown* 750 (F, MIN, MO, NY, US); Glen Blair, *Eastwood & Howell* 2665 (A); Elk Creek, *Leiberg* 4190 (US). MONTEREY CO.: Salinas Valley, *Vasey* 86 (F, US); Tassajara Hot Springs, *Elmer* 3178 (MIN, MO, US); Carmel Highlands, *C. E.* 8296 (MIN); Big Sur, *Eastwood* 14026 (A); Pacific Grove, *Demaree* 7257a (NY). NAPA CO.: Calistoga, *Greene, s.n.* (ND-G); Napa Valley, *Torrey* 74 (NY); Mt. St. Helena, *Eastwood* 6867 (A). NEVADA CO. 120° 39′ W. Long., 39° 20′ N. Lat., *collector unknown* (ND-G). ORANGE CO.: Santa Ana Mts., *Rice, s.n.* (MSC). RIVERSIDE CO.: San Jacinto, *Leiberg* 3117 (US). SACRAMENTO CO.: Sacramento, Pocket Road, *Copeland, s.n.* (MSC); Folsom, *Copeland* 1606 (GH). SAN BENITO CO.: Tres Pinos, *Eastwood* 6888 (A, US); The Pinnacles, *Eastwood* 6729 (A). SAN BERNADINO CO.: San Bernadino, *Wright* 207 (GH). SAN DIEGO CO.: San Diego, *Palmer* 42 (G, GH, MO, US); Cuyamaca Peak, *Hitchcock, s.n.* (US); Alpine, *Mearns* 4019 (NY, US); Descamso, *Eastwood* 9075 (GH). SAN FRANCISCO CO.: San Francisco, Lincoln Park, *Eastwood, s.n.* (US). SAN LUIS OBISPO CO.: Morro Bay, *Eastwood* 14254 (A); Avila, *Eastwood* 13788 (A); Cambria, *Eastwood* 13616 (A). SAN MATEO CO.: Higgins Creek Road, east of Half Moon Bay, *Mason, s.n.* (MSC); Corte Madera Creek, *Wiggins, s.n.* (MSC); San Carlos River, *Eastwood* 12414 (A). SANTA BARBARA CO.: *Elmer* 3940 (F, GH, GH, MIN, MO, US, NY); Carpinteria, *Dickover, s.n.* (US); Santa Cruz Island, *Eastwood* 6403 (A); vicinity of Smuggler's Cove, Santa Cruz Island, *Abrams and Wiggins* 204 (A, GH); Montecito Valley, *Bingham* 142 (KSC). SANTA CLARA CO.: Stanford University, *McMurphy* 56 (MIN, MO, ND-G, NY, OSC, GH, US); Gilroy Hot Springs, *Eastwood and Howell*

4304 (A); Clarita Vineyard, Black Mts., *Elmer, s.n.* (MIN, MO, NY, OSC, US); Los Gatos, *Heller* 7327 (A, F, MO, NY, US, GH); Beels Station, *Goldman* 1290 (US); New Almaden, *Torrey* 74 (GH, NY); Saratoga Springs, *Leeds, s.n.* (F); San Jose, *Eastwood* 11238 (A); Mt. Hamilton, *Eastwood* 12420 (A); Mayfield, *Wiggins* 9221 (A); west slopes of Sierra Nevada, east of Palo Alto, *Wiggins, s.n.* (MSC); bank of San Francisquito Creek, Palo Alto, *Wiggins, s.n.* (MSC). SANTA CRUZ CO.: Santa Cruz, *Ball, s.n.* (US). SHASTA CO.: SE slope of Long Valley Mt., *Griffin* 1143 (MSC); gulch north of Pit River, *Griffin* 1156 (MSC); Cow Creek Mts., *Baker and Nutting* (ND-G). SIERRA CO.: locality unknown, *Lemmon* 1032 (GH). SISKIYOU CO.: Hornbrook, Klamath River, *Abrams* 9900 (MO, RM); Shasta Pine, *Butler* 1034 (E); Shasta Springs, *Eastwood* 6694 (A). SONOMA CO.: Petaluma, *Congdon, s.n.* (MIN); Geyserville, *Torrey, s.n.* (NY). SUTTER CO.: Yuba City, Marysville Buttes, *Ferris* 651 (MIN, NY). TRINITY CO.: Tangle Blue and Scott Mt. creeks, *Howell* 12826 (A). TULARE CO.: Eshom Creek, *Clemens s.n.* (RM); Kaweak River, *Woolsey, s.n.* (GH). VENTURA CO.: Foster Park, *Eastwood* 5010 (A); Sulphur Mt., *Abrams & McGregor* 46 (A, ARIZ, GH, NY, OSC, US). YOLO CO.: chamise chapparral along Buckeye Creek, near Dunnigan, *Gillis* 4836 (MSC); Putah Canyon, *Dickson* 24 (OSC); Wintere, *Eastwood* 14202 (A). **Oregon.** BENTON CO.: Corvallis, *Steward* 6863 (NY, OSC); McFadden Marsh, north of Bellfountain, *Steward* 7011 (NY, OSC); MacDonald Forest, *Ishimoto* 3077 (OSC). CLACKAMUS CO.: Willamette Slough, *Howell & Howell, s.n.* (NO); Willamette Hills, *Mulford, s.n.* (GH, MO, NY); COOS CO.: Coos Bay, *House* 4746 (US). DOUGLAS CO.: Umqua River, *Engelmann & Sargent, s.n.* (A, MO); 5 miles south of Roseburg, *Gillis* 4163 (MSC); between Tiller and Drew in foothills of Cascades, 1200 feet, *Gillis* 4169 (MSC); Peel, *Applegate* 2700 (US); Oakland, *Hurst* 44 (A); near Tyee Mt., *collector unknown* (OSC). GILLIAM CO.: Blalock along Columbia gorge, *Cooke* 12116 (WTU). GRANT CO.: Blue Mts., *Hooker, s.n.* (GH). HOOD RIVER CO.: between Hood River and Mosier, *Suksdorf* 2102 (A); Mt. Hood, *Savage, Cameron, & Lenocker, s.n.* (MO); Hood River, floodplain of Hood River, *Gillis* 4246 (MSC); 2 miles south of Hood River, *Gillis* 5231 (MSC). JOSEPHINE CO.: Grants Pass, *Jack, s.n.* (A); Kerby, *Thompson* 4053 (MO, US). LANE CO.: Cheshire along highway 36, *Gillis* 4156 (MSC); Mapleton, *Gillis* 4159 (MSC). MARION CO.: Jefferson, south slope of Knox Butte, *Gillis* 4151 (MSC); Salem, near Morningside Grade School, *Matthews, s.n.* (OSC). MULTNOMAH CO.: Rocky Butte, *collector unknown* (F); Bridal Veil, *Smith* 3117, (F, NY); Portland, *Walpole* 44 (US). WASCO CO.: the Dalles, *Gillis* 4222 (MSC). WASHINGTON CO.: Scroggins Creek, *Thompson, s.n.* (MO). UNCERTAIN LOCALITY: *Hall* 82 (A, GH, F, MIN, MO). **Washington.** CLARK CO.: ½ mile east and ½ mile north of Crawford, *Gillis* 5274 (MSC). COWLITZ CO.: Kalama, *Gillis* 4263 (MSC); Kelso,

Palmer 37961 (A, MO). KING CO.: Seattle, Alki Point, *Gillis* 4251 (MSC); Mercer Island, *collector unknown* (F). KITSAP CO.: Orchard Point, *Piper, s.n.* (A). KLICKITAT CO.: terrace of Klickitat River near confluence with Columbia, *Gillis* 5238 (MSC). PIERCE CO.: between Steilacoom and West Tacoma, *Gillis* 4258 (MSC).

CANADA: **British Columbia.** Fort Vancouver, *Douglas, s.n.* (K); Vancouver Island, *Anderson, s.n.* (GH).

MEXICO: **Baja California Norte:** Ensenada, *Wiggins & Gillespie* 3997 (A, GH, MO, NY); El Rosario, *Brandegee, s.n.* (GH).

The first binomial of *Toxicodendron diversilobum* was *Rhus lobata* Hooker, but this name was a later homonym of Poiret's *Rhus lobata*, a non-toxic sumac from the Canary Islands. Therefore, in searching for the next epithet at the species level, one finds *Rhus diversiloba* to be satisfactory. When the name is transferred to *Toxicodendron*, the epithet *lobatum* appears to have priority, but Arts. 64 and 72 of the Code (Lanjouw et al., 1966) preclude the use of illegitimate epithets, even in combination with another generic name. The earliest, available, legitimate epithet of specific rank, then, is *diversiloba.*[14] Under its name *Rhus diversiloba*, the plant is occasionally found in print as *R. diversifolia*, a misprint probably first published by Engler in DeCandolle (1883, p. 305). Whereas the type specimen of *Rhus lobata* Hook. indicates that the species is "plentiful" on Vancouver Island, the species is rare to the point of being almost unknown in British Columbia today.

Greene did not specify where his type for *Toxicodendron comarophyllum* was located, but most of the type specimens for poison-ivy and poison-oak taxa he described are at the Smithsonian Institution; therefore, the specimen cited as the type is the one located there. A probable isotype at the Missouri Botanical Garden has a different collection num-

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[14]Initially a combination of *Toxicodendron* with *lobatum* was chosen in connection with this study and all herbarium material examined at that time was so annotated. I am grateful to Dr. Robert Thorne for pointing out this error before this manuscript went to press. Material thus annotated should be considered to be *Toxicodendron diversilobum* (T. & G.) Greene until such time as the corrected annotations shall be made.

ber, but presumably comes from the same gathering; its label data are the same. Jepson (1936) clarified the collection site by indicating that it was "at the foot of Ballena grade, San Diego."

In regard to *Toxicodendron oxycarpum,* Greene places emphasis on the wrinkled nature of the fruits, but this is a common phenomenon of herbarium specimens bearing unripe fruits; when they have not yet reached full growth, the exocarps wrinkle in the drying process. Greene's notation that the branching of the inflorescence is sparse certainly calls attention to a chance character of this single specimen and refers to a character of no genetic significance. Lkewise, the importance Greene attaches to the pendulous nature of the fruits is probably not significant.

Greene's choice of specimens for his *Toxicodendron isophyllum* leaves much to be desired. His descrption and the type specimen do not agree in most characteristics. The leaflets are not "all three sessile"; there is no epicarp present from which to determine that it is "muricate-punctate" and "pubescent." Perhaps it was available when Green described the species.

As with other types, Greene did not indicate the location of the type of *Toxicodendron dryophilum.* Representatives of the type collection are at Notre Dame (Herbarium Greeneanum) and at the Smithsonian. He wrote "type" on the specimen at ND-G even though part of the description ("reported to sustain itself to the height of 20 feet on oak trees") comes from the label data present only on the specimen at US. I have chosen the Notre Dame specimen as the lectotype. Greene's description "never panicled fruits seldom more than 2 or 3 to each raceme" is not borne out by the type collection. The "wrinkling of the epicarp," which seems to have been firmly implanted in Greene's mind as significant in this and several other species of the complex, is typcal for dried immature fruits.

The type collection of *Toxicodendron vaccarum* is indicated as having come from Shasta County, California, from the Cow Creek Mountains. In order to locate the site of collection more precisely, I have contacted several persons

in California, especially in Shasta County, to ascertain the precise location of these mountains. No one has been able to give me any information about any mountains of that name in Shasta County. Such mountains are known in Mendocino and Lake Counties, but not in Shasta County.

McNair's name *Rhus diversiloba* f. *radicans* poses some perplexing problems. He indicated that it was synonymous with *Toxicodendron dryophilum* Greene; therefore it should have the same type as *T. dryophilum*, but he proceeded to write on the specimen (*Millspaugh* 4734) at the Field Museum "forma radicans McNair type." Although he indicated no type in his publication, he apparently intended the Millspaugh specimen to be a representative one. He was attempting to recognize nomenclaturally a form of western poison-oak which had the climbing habit, stating that "taxonomic recognition as a form may be desirable" (McNair, 1925). The ability to climb appears to be general in this species, so that the climbing forms are not genetically different from suffrutescent ones and therefore deserve no nomenclatural recognition.

McNair later (1936) gave a form name to a five-leaflet specimen of Western poison-oak. A type specimen again was not cited. Of the seven specimens which he lists as having the five-leaflet trait, I have chosen the first-mentioned as lectotype: *Wood, s.n.* 1866. This form also deserves no segregate name since there is variability from branch to branch even on the same shrub or vine. Western poison-oak, even more than its eastern counterparts, may frequently have additional leaflets, the author having seen up to eleven (*Gillis* 4874, Glenn Co., California, MSC-165725). Barkley (1936) has also described a five-leaflet poison-ivy, but did not give it a name. Vines (1943) did assign a name to a five-leaflet form (*Rhus toxicodendron* var. *multifolia*) which he later abandoned (see discussion under *T. radicans* subsp. *pubens*).

Western poison-oak was not among the plants mentioned by the early explorers of the American West. Although the Spanish padres and Conquistadores described the wild life they encountered in California in the fifteen and sixteen

hundreds, poison-oak is not among the species discussed. It is difficult to imagine that this plant could have been as abundant as it is now, and yet escape detection, particularly in view of its toxic properties. A possible conclusion is that the plant was less common several centuries ago. Because *Toxicodendron diversilobum* is a plant which increases in abundance with disturbance, it is likely that it has become more abundant with the activities of man in clearing the countryside, especially changing fire frequency. Its distribution in Baja California, where men's activities have been relatively small, is still sparse, although in that region low rainfall also plays a significant role in its scarcity.

The distribution of the plant is throughout much of California west of the Sierras and the desert. In Oregon and Washington, it is channeled between the Coast Ranges and the Cascades. It is known from only one region on the east flank of the Cascades where James R. Griffin collected it for me in Shasta County, California, on the southeast slope of Long Valley Mountain and on slopes above the Pit River. Local lore in southern Oregon has it that neither poison-oak nor rattlesnakes occur east of the Rogue River. The highest elevation in the Cascades from which *Toxicodendron diversilobum* has been collected is in Douglas Co., Oregon, between Tiller and Drew, at 1200 feet.

Like its counterparts elsewhere in the United States, *Toxicodendron diversilobum* is highly variable, especially in leaflet shape. Its leaflets may be as deeply lobed as are the leaflets of male clones of *T. toxicarium*, thus resembling the leaves of *Quercus alba*, but more often they resemble the leaves of one of the western oaks, such as *Q. agrifolia*. At times, they are even without any evident lobes at all and may be only undulate in leaflet margin. I have been unable to correlate geographical or regional factors with variation in leaflet shape except that sun leaves are normally much larger than shade leaves. The fruits are among the largest of Western Hemisphere *Toxicodendron* species, with deeply furrowed striations in the mesocarp and short, abundant trichomes on the exocarp.

Toxicodendron diversilobum is far less common in Wash-

ington than farther south. In some counties, it is unquestionably scarce. On disturbed sites in the Seattle area (Alki Point, for example), it is abundant enough that municipal authorities have seen fit to erect a sign warning the populace that the hillside is covered with poison-oak, rather than clear away the menace.

In the Columbia River gorge, the ranges of *Toxicodendron rydbergii* and *T. diversilobum* overlap. Intergrades are known from Hood River to The Dalles from the washes and rills of the basaltic hills through which the river has cut; on the Washington side of the river, such intergrades are known from the confluence of the Klickitat and the Columbia east to the vicinity of the John Day Dam. The zones of overlap in range and apparent hybridization between these two species seems to cover about 23 miles along the Oregon shore and about 43 miles along the Washington shore of the Columbia. It was from this region that the type specimens of *T. coriaceum* and *T. lobadioides* came, presumably from the same population (one flowering and one fruiting). In naming these species, Greene recognized that they were different from other named taxa, but did not realize that they might be hybrids, which they probably are (see discussion under section on Hybrids, Crosses, and Intergrades).

Habitats for *Toxicodendron diversilobum* are nearly as catholic as those of any other taxon in this complex. Jepson (1936) described its range of habitats in detail:

"In San Diego County it is associated with characteristic woody species of cismontane Southern California, all of which are wholly different from the associated species in various northern regions, as the Sierra Nevada foothills or Vaca Mountains, these in each case being in the main different from each other yet again from the associated species in the case of the Redwood belt. It has a wider geographic range than any California shrub and grows under a greater variety of soil conditions than any other; though usually preferring good soil or rich loams, it grows in blue adobe, in saline soils, in gray clays, in sandy flats, in heavy gravel deposits and in the crevices of outcropping

rock piles. It is also adapted to a greater range of rainfall and temperature than any other California shrub and is especially remarkable for its extreme shade tolerance and its tolerance of intense insolation. In common with all other woody vegetation it is absent from wide areas on the inner foothills and the plains of the Great Valley. Its preferred habitats are moist slopes in the hills; in such situations it is seldom lacking. It is also curious to add that of all native woody vegetation about the great Keswick smelter on the upper Sacramento River, the species least injured by smelter fumes was *Rhus diversiloba*; at a given station near the smelter it lived in spite of the conditions, while practically all other species were seriously destroyed or in the main destroyed."

"In number of individuals Poison Oak exceeds, in our judgment, any other shrub species in California. While the vast colonies of *Adenostoma fasciculatum* or the mesa growths of *Larrea tridentata* are impressive to the eye, *Rhus diversiloba* occurs over a much larger area than either. It is often an unobtrusive shrub — scarcely noticed in many formations and yet the individuals are really very numerous. When, for example, a Mendocino hillside wooded with *Arbutus menziesii, Quercus douglasii* and various shrubs is cleared, the response of Poison Oak by crown-sprouting tells the story of its abundance. It grows in the openly oak-wooded foothills, in Douglas Fir forest, in the Redwood belt, along river banks and "bottoms" and even in salt domes, often in chaparral and rarely in chemisal. In altitudinal distribution the species exists from sea-level to about 5000 feet. In the southern Sierra Nevada it grows as high as 4760 feet, and it is not found on the Yosemite Valley floor, but occurs in Hetch-Hetchy and on the slopes of Francheria Mt. above Hetch-Hetchy at about 4500 feet; in Butte Co. it is found as high as 3800 feet."

No voucher collections have been seen that substantiate some of the extremes to which Jepson alludes, but suffice it to say, *Toxicodendron diversilobum* is very abundant. It is found through central and western California and in the Willamette Valley of Oregon. It is less common, even

scarce, north of the Columbia River except for very local populations. The disturbance due to the activities of European settlers in developing California may account for the tremendous increase in abundance of this plant.

Contrary to the report of Jepson (*loc. cit.*), I have found that it is now quite abundant, at least locally, in the chamise chaparral. It grows well with *Quercus douglasii, Ceanothus spp.*, and *Pincus sabiniana.* It also occupies ruderal environments especially those susceptible to fire, provided some moisture is available during the long, dry summer. In Oregon it is abundant in almost any lowland or mesic woods in the Willamette Valley and at elevations up to 1250 meters in the Cascade foothills. Its common associates are *Pseudotsuga menziesii, Quercus garryana,* and *Berberis aquifolium.*

4. **Toxicodendron radicans** (L.) Kuntze, Rev. Gen. Pl. Pt. 1, p. 153. Pl. 26, fig. 2. 1891. *Rhus radicans* L., Sp. Pl. 1: 266. 1753.

Vine, shrub, rarely an epiphyte or tree, with slender, glabrous to puberulent branches, often with brown aerial roots; rhizome creeping. Leaflets 3 or rarely 5 (-7), ovate to elliptic, entire or irregularly serrate, dentate, lobed, or deeply incised; acute to acuminate or cuspidate at apex, glabrous to puberulent above, often with minute curled hairs on upper mid-vein near the base, glabrous to velutinous below, often with tufts of hairs in main vein axils below; petiole 2-20 cm long; lateral leaflets mostly inequilateral, 2.5-18 cm long, 1.0-10.0 cm broad, truncate to obtuse, subcuneate or attenuate; petiolules less than 0.1-1.2 cm long; leaflets often subsessile; terminal leaflet blade 3.0-20.0 cm long, 1.5-13.0 cm broad, truncate, obtuse, subcuneate, or attenuate at the base, petiolules 0.3-6.0 cm long; leaflets attached in palmate fashion when leaf is trifoliolate, pinnate when leaf is composed of more than 3 leaflets. Inflorescence a lateral paniculate thyrse, up to 1 dm long; pedicels pilose, 2-5 mm long; bracts deltoid to lanceolate, 0.7-10 mm long, 0.5-3 mm broad at the widest point, glabrate, ciliate, deciduous; sepals 5, deltoid-ovate, 1 mm

long, 2-4 mm broad, glabrate; petals 5, cream to yellow-green, pinnately dark-veined, oblanceolate, glabrous, 2-5 mm long, 2-5 mm broad, reflexed in male, recurved in female, larger in male than in female, anthers lanceolate, 1-1.5 mm long, 0.5-1.1 mm broad, filaments linear-subulate, 1.3-1.8 mm long. Drupe hard, cream, yellow, or tan, globose to globose-reniform, sometimes laterally flattened, 0.25-0.7 cm across, 0.15-0.65 cm broad, with exocarp glabrous to bristly, becoming papery upon ripening, readily separating from the mesocarp, later deciduous; mesocarp black-striate in white, waxy matrix; endocarp dun-colored, bony. Bark gray-brown to red-brown on new wood, becoming gray on older wood; leaf scars V- or U-shaped wth several bundle scars; lenticels usually conspicuous. Buds stalked, naked, mucronate, brown, covered with a brown wooly pubescence. Autumn coloration yellow to orange, occasionally red or bronze.

Common names: poison-ivy, markweed, poison-mercury, herb à la puce, cow-itch, Gift-sumach.

Toxicodendron radicans is one of two species of the New World (poison-ivy) and of Eastern Asia (tsuta-urushi). It is the most common and most widespread species in the Anacardiaceae. It is distributed from southern Canada to western Guatemala, the eastern third of the United States and throughout Mexico, on Bermuda, and in the western Bahamas, in Japan, western and central China and Taiwan, the Kurile Islands and Sakhalin of the U.S.S.R.

The plant is primarily scandent, but may also grow as a shrub. All taxa within this species produce aerial rootlets but will develop into large shrubs if there is nothing to climb, or if the supporting object upon which the climbing began is removed. Its closest relatives are *Toxicodendron diversilobum* and *T. rydbergii*. The plant is highly variable, much of the literature being replete with names of taxa which have few if any significant genetic differences. Because the nomenclature is very complex, it is discussed with each subspecies recognized in this study. The species consists of nine subspecies.

Fig. 32. *Toxicodendron radicans* ssp. *radicans*. Type of *Rhus radicans* L. The Linnaean Herbarium.

Fig. 33. *Toxicodendron radicans* subsp. *radicans*. Type of *Rhus radicans* var. *vulgaris* forma *intercursa* Fernald, *Fernald, Long & Smart* 5832.

4a. **Toxicodendron radicans** (L.) Kuntze subsp. **radicans.** Figs. 32, 33.

Toxicodendron radicans (L.) Kuntze, Rev. Gen. Pl. pt. 1, p. 153. Pl. 26, fig. 2. 1891. *Rhus radicans* L., Sp. Pl. 1: 266. 1753. *Rhus radicans opacum* Aiton, Hort. Kew. 1: 367. 1789. *Rhus toxicodendron* var. *radicans* Eaton, Man. Bot., p. 400. 1789. *Rhus scandens* Salisbury, Prodr., p. 170. 1796. *Rhus radicans* var. *toxicodendron* Persoon, Syn. Pl. p. 325. 1805. *Philostemon radicans* Raf., Fl. Ludov., p. 107. 1817. *Rhus toxicodendron radicans* Torrey, Fl. North. Mid. U.S., p. 324. 1824. *Toxicodendron radicans normale* Kuntze, Rev. Gen. Pl. pt. 1, p. 153. 1891. *Rhus toxicodendron* a *radicans* Dippel, Handb. der Laubholzk., p. 376. 1892. *Rhus toxicodendron* f. *radicans* McNair, Publ. Field Mus. Nat. Hist. 225, Vol. 4: 68. 1925. *Rhus toxicodendron* subsp. *radicans* Clausen, Mem. Cornell Univ. Agric. Exp. St. 291: 8. 1949. Type: "Habitat in Virginia, Canada." (LINN 378.14, lectotype of Brizicky, 1963; GH, MSC, photographs of type).

Toxicodendron glabrum Mller, Gard. Dict. Art. *Toxicodendron*, No. 3. 1768, non *T. glabrum* (L.) Kuntze, Rev. Gen. Pl. pt. 1, p. 153. 1891 (= *Rhus glabra* L.). *Rhus humilis* (as *humile*) Salisbury, Prodr., p. 170. 1796. *Rhus radicans lucidum* Aiton, Hort. Kew. 1: 367. 1789. Type: "Dill. Elth., *loc. cit.*" (OXF, lectotype).

Rhus toxicodendron var. *microcarpon* Michx., Fl. Bor.-Am., p. 395. 1803. *Rhus toxicodendron microcarpum* Pursh, Fl. Am. Sept. 1: 205. 1814. *Rhus radicans* var. *microcarpon* (Michx.) DC., Prodr. 2: 69. 1825. *Rhus toxicodendron* subsp. *microcarpon* (Michx.) Engler in DC., Monog. Phaner. 4: 395. 1883. *Rhus microcarpa* Steudel, Nom. Bot. ed. 2: 694. 1841. *Toxicodendron radicans* var. *microcarpon* (Michx.) Farwell, Amer. Midl. Naturalist 12: 125. 1930. Type: "Hab. in Carolina inferiore et Georgia." (P, lectotype).

Rhus blodgettii Kearney, Bull. Torrey Bot. Club 21: 486. 1894. *Toxicodendron blodgettii* (Kearney) Greene, Leafl. Bot. Observ. Crit. 1: 126. 1905. Type: *Blodgett, s.n.*, Pine Key, near Key West, Monroe Co., Florida, (NY, lectotype of Barkley, 1937).

Rhus floridana Mearns, Proc. Biol. Soc. Wash. 15: 149. 1902. Type: *Hitchcock* 39, Hammocks, Alva, Lee County, Florida, A.S. (US-387083, holotype; F-101118, GH, MIN-149688, MO-1773781, NY, isotypes).

Toxicodendron goniocarpum Greene, Leafl. Bot. Observ. Crit. 1: 125. 1905. Type: *Lucia McCulloch* 45, Lake City, Columbia Co., Florida. 25 June 1901. (US-440443, holotype; FLAS-16153, isotype; US-440444, probable isotype).

Rhus toxicodendron f. *malacotrichocarpum* Moore, Rhodora 11: 163. 1909. *Rhus radicans* f. *malacotrichocarpa* (Moore) Fernald, Rhodora 43: 592. 1941. Type: *E. B. Chamberlain and G. E. Dinsmore* 832, in and growing over bushes, Pemaquid Beach, Bristol, Lincoln Co., Me. 9 Sept. 1898. (GH, holotype).

Rhus littoralis Mearns, Proc. Biol. Soc. Wash. 15: 148. 1902. *Rhus radicans* var. *littoralis* (Mearns) Deam, Fl. Indiana, p. 651. 1924. *Toxicodendron radicans* var. *littoralis* (Mearns) Barkley, Ann. Missouri Bot. Gard. 24: 434. 1937. Type: *Edgar Mearns* 233, Newport, Rhode Island, Sept. 10, 1901. (US-403300, holotype; US-1317009, US-403299, NY, isotypes).

Rhus radicans var. *vulgaris* f. *intercursa* Fernald, Rhodora 43: 592. 1941. Type: *Fernald, Long, and Smart* 5832, Virginia, deciduous woods, Curles Neck Farm, Henrico Co., June 21, 1936. (GH, holotype; NY, isotype).

Terminal leaflet obtuse, subcordate, or truncate at the base, with widest part generally below center; tufts of hairs in vein axils of leaflets hyaline or straw-colored, occasionally red-brown; blade 2.5-17.0 cm long, 2-13 cm wide, petiole 2.0-20.0 cm long; terminal petiolule 0.5-6 cm long; fruits globose, 3-6.5 mm broad, puberulent, scabrous, or papillose.

Distribution: United States, states bordering on the Atlantic Ocean, southern Maine southwest, west to Appalachians, Ozarks, and East Texas; Bahama Islands; Bermuda. (Fig. 34).

Representative specimens. UNITED STATES. **Alabama.** AUTAUGA CO.: Prattville, *Gillis* 4528 (MSC). BALDWIN CO.: Loxley Research plots, Stapleton, *Grelen, s.n.* (FLAS). CLARKE CO.: Jackson, *Gillis*

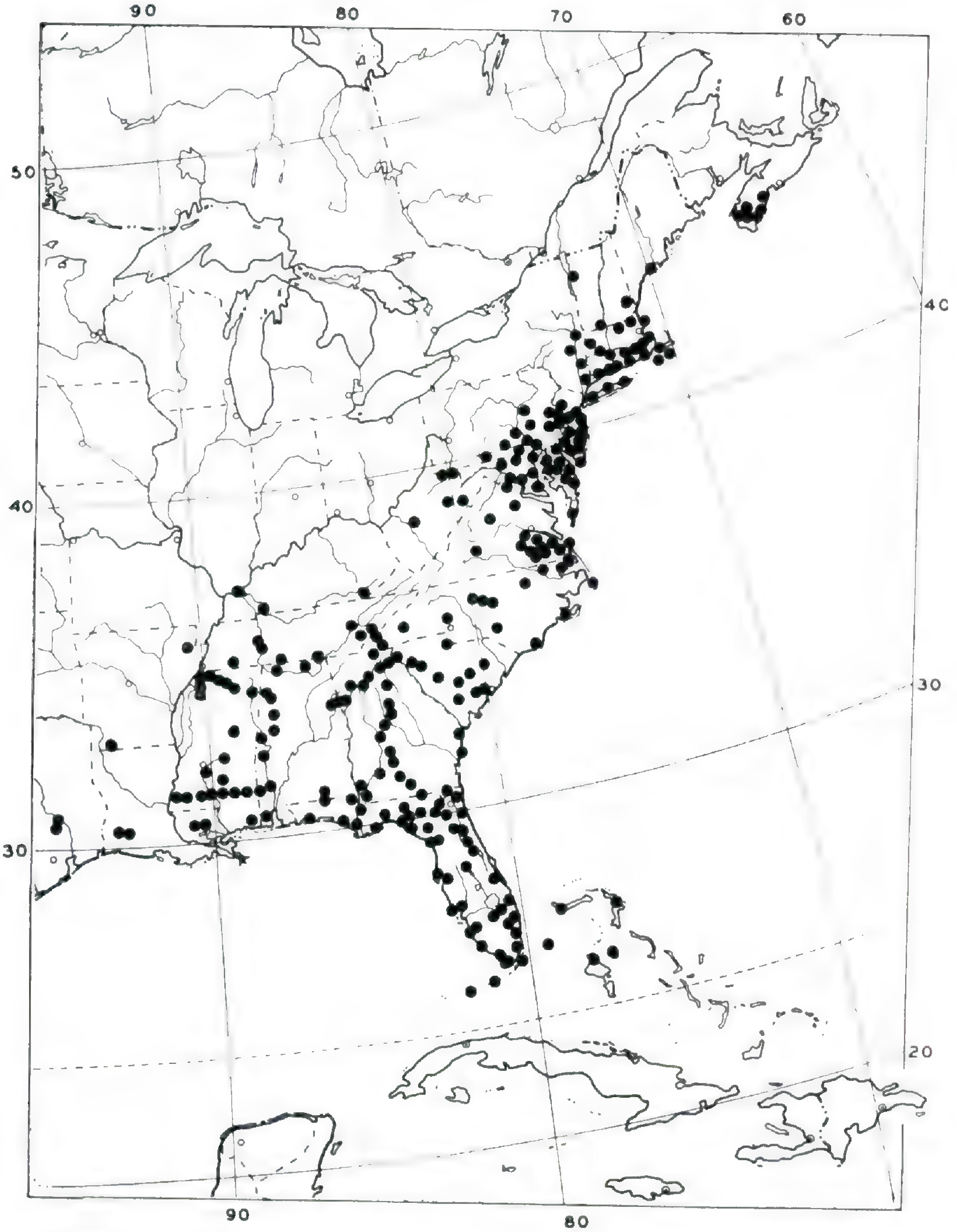

Fig. 34. Distribution of *Toxicodendron radicans* subsp. *radicans*.

6019 (MSC). CLEBURNE CO.: 6 miles NNW of Edwardsville, *Donahue* 248 (MSC). COLBERT CO.: Sheffield, river bank, *Bartlett* 3370 (MSC, MICH). ELMORE CO.: Elmore, *Gillis* 4525 (MSC). FAYETTE CO.: southern edge of Fayette Experimental Forest, *Gillis* 6037 (MSC). GREENE CO.: 2 miles north of Forkland, *Gillis* 6024 (MSC). HALE CO.: Talladega National Forest, Payne Lake Recreational Area, *Donahue* 246 (MSC). JEFFERSON CO.: flat woods between Mobile Junction and

McCalla, *Bartlett* 3350 (MSC, MICH). LEE CO.: Auburn, *Earle, s.n.* (NY). MACON CO.: Tuskegee, *Gillis* 4506 (MSC). MADISON CO.: Huntsville, *Gillis* 4550 (MSC). MARION CO.: 9.1 miles south of Hamilton, *Gillis* 6039 (MSC). MOBILE CO.: Chunchula, *Shinners* 29301 (SMU). SHELBY CO.: ½ mile SW of Columbiana, *Donahue* 247 (MSC). TUSCALOOSA CO.: Tuscaloosa on river bluff, *Bartlett* 3314 (MICH, MSC). UNION CO.: 6.3 miles SE of New Albany, *Gillis* 6046 (MSC). WASHINGTON CO.: Chatom, *Gillis* 6015 (MSC). **Arkansas.** COLUMBIA CO.: Magnolia, *Demaree* 39203 (SMU). CRAIGHEAD CO.: Jonesboro, *Demaree* 3551 (SMU). DREW CO.: Monticello, *Demaree* 13692 (MO). GARLAND CO.: near Hot Springs, *Runyon* 1211 (NY). HEMPSTEAD CO.: Fulton, *Palmer* 5416 (A, MO, US). HOT SPRINGS CO.: Magnet Cove, *Demaree* 14802 (GH, MO, NY). **Connecticut.** FAIRFIELD CO.: Bridgeport, *Eames, s.n.* (US); Easton, *Johnson* 447 (F). LITCHFIELD CO.: without definite locality, *Weatherby* 5294 (US). MIDDLESEX CO.: Westbrook, *Gillis* 4112 (MSC). NEW LONDON CO.: Groton, *Jansson*, s.n. (OSC); WINDHAM CO.: *Thompson, Churchill & Lane, s.n.* (MO). **Delaware.** KENT CO.: Leipsic, *Laisen* 714 (GH). NEW CASTLE CO.: New Castle, *Tidestrom* 11547 (GH). SUSSEX CO.: *Fogg* 11186 (GH); Milford, *Gillis* 3848 (MSC). **District of Columbia.** Brookland, *Bartlett* 1788, 1789, 1790, 1791, 1793, 1795 (MICH, MSC, SMU). Columbian Formation, *Boettcher* 250 (A, F, GH, MO, RM). **Florida.** ALACHUA CO.: Gainesville, *O'Neill, s.n.* (MO); Gainesville, periphery of golf course on Newberry Road, *Gillis* 3932 (FLAS, MSC); Devil's Millhopper sink-hole, 12 miles NW of Gainesville, *Gillis* 4345 (MSC). BAKER CO.: titi pond, Manning, *West & Arnold, s.n.* (FLAS). BAY CO.: St. Andrew's Bay, *Benker* 3506 (NY). BRADFORD CO.: Santa Fe banks south of Hampton, *West & Arnold, s.n.* (FLAS). BREVARD CO.: Cocoa, *Gillis* 4356 (MSC). BROWARD CO.: Hugh Taylor Birch State Park, Fort Lauderdale, *Roestad, s.n.* (FLAS). CITRUS CO.: Red Level, *West & Arnold, s.n.* CLAY CO.: Goldhead Branch State Park, *West, s.n.* (FLAS). COLLIER CO.: Everglades, Miles City near fire tower, *Gillis* 4480 (MSC); 7.3 miles NW of Copeland, Fahkahatchee Strand, *Ward & Botany Class* C-6 (FLAS). COLUMBIA CO.: Lake City, *McCulloch* 45, 46 (FLAS, US). DADE CO.: Homestead, *Small & Wilson, s.n.* (F, NY); Roberts Island, *Small* 7387 (NY); Long Pine Key, *Traverse* 590 (GH); Sykes Hammock, Everglades Keys, *Small & Mosier* 5482 (FLAS, GH, NY, US). DESOTO CO.: Hammock, west edge of Arcadia, *Botany class* B-5 (FLAS). DIXIE CO.: Hammock, 1 mile NE of Jena, *Pasture Survey, s.n.* (FLAS). DUVAL CO.: Jacksonville, *Curtiss* 4646 (MO, US). ESCAMBIA CO.: Santa Rosa Island, *Blair, s.n.* (FLAS). FRANKLIN CO.: St. Vincent Island, *McAtee* 17388 (US). GLADES CO.: west of Lake Okeechobee, *Small & DeWinkeler, s.n.* (NY). GULF CO.: Wewahitchka, Dead Lake, *Demaree* 50426 (MSC). HAMILTON CO.: Bayhead 3 miles south of Jennings, *West & Arnold, s.n.* (FLAS). HIGHLANDS CO.: Lake Placid, *Craighead, s.n.* (MSC); Hillsborough, Tampa Bay shore,

Rolfs 247 (F, MO). JACKSON CO.: Blue Springs north of Marianna, *Exploration Party 1937, s.n.* (FLAS). LAFAYETTE CO.: Opposite Branford on Suwannee River, *West & Arnold, s.n.* (FLAS). LEE CO.: Alva, *Hitchcock* 39 (F, GH, MIN, MO, NY, US); Sanibel Island, *Cooley* 2499 (FLAS, GH, NY, US). LEON CO.: Woodville, *Godfrey & Morrill* 53026 (FSU, GH, NY). LEVY CO.: 2 miles south of Gulf Hammock, *Pasture Survey, s.n.* (FLAS). MADISON CO.: Sirmans, *Palmer* 27268 (A, MO). MANATEE CO.: Long Boat Key, *Gillis* 3939 (MSC); mouth of Manatee River, *Rugel* 79 (BM). MARION CO.: bayhead, 3 miles south of range Springs, *West & Arnold, s.n.* (FLAS); Eureka on Oklawaha River, *Godfrey & Houk* 62806 (MSC); Silver Springs, bank of Silver River, *Gillis* 6594 (MSC). MARTIN CO.: Lake Okeechobee, *Moldenke* 5440 (NY). MONROE CO.: Key West, *Blodgett, s.n.* (NY); Flamingo, *Craighead, s.n.* (MSO); Big Pine Key, *Ward* 4330 (FLAS); NASSAU CO.: Julee, *Gillis* 3958 (MSC). OKALOOSA CO.: Bolton Creek swamp, *Tyson* 314 (FLAS). ORANGE CO.: near Christmas, *Gillis* 6884 (MSC); OSCEOLA CO.: outskirts of Intercession City, *Gillis* 6468 (MSC). PALM BEACH CO.: Palm Beach, *Garvens, s.n.* (F). PINELLAS CO.: St. Petersburg Beach, *Gillis* 6347 (MSC). PUTNAM CO.: west of Mud Springs, Welaka, *Laessle, s.n.* (FLAS). ST. JOHNS CO.: 10 miles west of St. Augustine, *West & Arnold, s.n.* (FLAS); ST. LUCIA CO.: along S-607, 1 mile west of Indio Road, *Gillis* 6894, (MSC). SUMTER CO.: Rutland, hammock near Withlacoochee River, *West & Arnold, s.n.* (FLAS). TAYLOR CO.: Half Mile Rise on Aucilla River, *Exploration Party 1939, s.n.* (FLAS). UNION CO.: Cypress Pond Road, 2 miles south of Raiford, *West & Arnold, s.n.* (FLAS). VOLUSIA CO.: 3 miles west of Stetson University, *Prichard* 533 (FLAS); Cypress hammock about 5 miles NE of Deland, *Rossbach & Prichard* 2039 (FLAS). WAKULLA CO.: 6 miles E of Sopchoppy, *Ward & Ford* 3631 (FLAS). **Georgia.** BIBB CO.: Macon, *Gillespie* 4889 (A, ND, SMU). BRYAN CO.: Richmond Hill, *Gillis* 4000 (MSC). CHEROKEE CO.: SW of Canton, *Donahue* 253 (MSC). CLARKE CO.: Athens, *James, s.n.* (MSC). COOK CO.: south of Lenox near Barneyville Road, *Gillis* 6582 (MSC); CRISP CO.: 0.5 mile north of Turner Co. line, *Gillis* 6578 (MSC). DECATUR CO.: Bainbridge, *Small, s.n.* (A, F, NY). DOOLE CO.: south of Unadilla, *Gillis* 6570 (MSC). DOUGLAS CO.: NE of Villa Rica, *Donahue* 252 (MSC). EARLY CO.: Blakely, *Gillis* 4502 (MSC). EMANUEL CO.: Swainsboro, *Gillis* 4968 (MSC). FLOYD CO.: Rome, Horseleg Mt., *Demaree & Lipps* 50109 (MSC). HABERSHAM CO.: between Clarkesville and Demorest, *Gillis* 6542 (MSC). HARALSON CO.: Tallapoosa, *Donahue* 250 (MSC). HOUSTON CO.: 6 miles north of Henderson, *Gillis* 6567 (MSC). JACKSON CO.: Commerce, *Gillis* 6577 (MSC). LUMPKIN CO.: Chattahoochee National Forest, DeSoto Falls Campground, *Donahue* 255 (MSC). MCDUFFIE CO.: Fall-line sand hills, vicinity of Thomson, *Bartlett* 1509, 1454, 1668, 1667, 1669, 1673, 1674, 1701, 1734, 1747 (MICH, MSC, SMU). MCINTOSH CO.: Sapelo

Island, *Gillis* 3961. MORGAN CO.: 6.6 miles north of Putnam Co. line, *Gillis* 6543A (MSC). PICKENS CO.: 5 miles west of Emma, *Donahue* 254 (MSC). TURNER CO.: 1 mile north of Inaha, *Gillis* 6580 (MSC). UNION CO.: 3 miles NW of Blairsville, *Donahue* 256 (MSC). **Kentucky.** BELL CO.: 0.5 miles NW of Fourmile, weathered rock cliff, *Gillis* 6540 (MSC). TRIGG CO.: 6 miles west of Cadez, *Donahue* 211 (MSC). **Louisiana.** Calcasieu Parish, Lake Charles, *Allison* 320 (US). FRANKLIN PARISH: Gilbert, *Gillis* 5951 (MSC). MOREHEAD PARISH: Jones, *Gillis* 5943 (MSC). NATCHITOCHES PARISH: *Palmer* 7353 (A, MO). RAPIDES PARISH: Valentine Lake, *Thieret* 17945 (MSC). SAINT TAMMANY PARISH: Covington, *Demaree* 50764 (MSC). **Maine.** LINCOLN CO.: Bristol, *Chamberlain* 832 (GH); Boothbay, *Fassett* 28979 (F, MO, SMU, WIS); Monhegan Island, *Churchill, s.n.* (MO). SAGADAHOC CO.: Five Islands, *Rehder* 1045 (A, US). YORK CO.: Isle of Shoals, *Howard & Wagenknecht* 5295 (A, MSC). **Maryland.** ANNE ARUNDEL CO.: Annapolis, *Tidestrom* 6639 (A, MO, US). BALTIMORE CO.: Sorrento, *Tidestrom & Bartlett* 7255 (SMU). CALVERT CO.: Cony Point, *Seymour* 17348 (SMU). CAROLINE CO.: Horse Point, Tuckahoe River, *Tidestrom* 11977 (US). FREDERICK CO.: Lewistown, *Gillis* 5695 (MSC); Hunting Creek, *Sullivan* 415 (ND). HARTFORD CO.: Spesukie Island, *Smith, s.n.* (US). MONTGOMERY CO.: Bethesda, *Bartlett* 1820 (MICH, MSC, SMU). PRINCE GEORGES CO.: Beltsville, *Hermann* 10866 (F); College Park, *Tidestrom* 7132 (US). ST. MARYS CO.: St. Mary, *Walker* 3954 (US). TALBOT CO.: Claiborne, *Tidestrom, s.n.* (US). WORCESTER CO.: Ocean City, *Fogg* 11464 (GH). **Massachusetts.** Barnstable Co.: Hyannis, *Fernald, Butters, & St. John* 15269 (GH). BERKSHIRE CO.: Williamstown, *Gillis* 4066 (MSC). BRISTOL CO.: Dighton, *Seymour* 18559 (SMU); Dartmouth, *Knowlton, s.n.* (MIN); New Bedford, *Greene, s.n.* (WIS); DUKES CO.: Oak Bluffs, *Seymour* 1262 (GH, NY, US); Gay Head, *MacKeever* 567 (MSC). ESSEX CO.: Rockport, *Rouleau* 1308 (ARIZ, E, F, FLAS, GH, MIN, MO, MSC, NY, OSC, RM, US, WIS). HAMPDEN CO.: Springfield, *Pillsbury, s.n.* (US). MIDDLESEX CO.: Lowell, *Beattie s.n.* (E, MO, OSC, SMU). NANTUCKET CO.: *Bicknell,* 5591 (NY). NORFOLK CO.: Stoughton, *Blake* 1294 (US); Brookline, *Rohson, s.n.* (A). PLYMOUTH CO.: Middleboro, *Murdoch* 527 (F). SUFFOLK CO.: Boston, *Williams, s.n.* (GH). WORCESTER CO.: Bolton, *Seymour* 6092 (WIS). **Mississippi.** BENTON CO.: near Union Co. line, *Gillis* 6047 (MSC). COVINGTON CO.: pine ridge west of Collins, *Gillis* 6006 (MSC); along route 35 below Bowie River, *Gillis* 6003 (MSC). FRANKLIN CO.: road to Clear Springs, *Gillis* 5975 (MSC); 3 miles from Roxie, *Gillis* 5873 (MSC). ITAWAMBA CO.: between Tremont and Fulton, *Gillis* 6043 (MSC). JACKSON CO.: Magnolia State Park, *Demaree* 31216 (SMU, TEX); Krede, *Demaree* 34912 (SMU). JEFFERSON DAVIS CO.: SE of Prentiss, *Gillis* 6002 (MSC). LAWRENCE CO.: Monticello, *Gillis* 5989 (MSC). LEE CO.: Tupelo, *Gillis* 6045 (MSC). LINCOLN CO.: New Prospect Baptist

Church, *Gillis* 5979 (MSC). MADISON CO.: without definite locality, *McDougall* 1590 (US). MARSHALL CO.: 2.4 miles SE of Holly Springs, *Gillis* 6048 (MSC). OKTIBBEHA CO.: Starkville, *Hill, s.n.* (ILL). PANOLA CO.: Sardis, *Broadhead* 36 (SMU). SMITH CO.: Marathon Lake Recreation Area, *Donahue* 242 (MSC). TATE CO.: Senatobia, *Gillis* 5908 (MSC). UNION CO.: 6.3 miles SE of New Albany, *Gillis* 6046 (MSC). **New Jersey.** ATLANTIC CO.: Mays Landing, *Fogg* 2129 (GH); Hammonton, *Gillis* 5649 (MSC). BERGEN CO.: without definite locality, *Oehler, s.n.* (NY). BURLINGTON CO.: Riverton, *Bassler* 69 (KSC); Mt. Holly, *Gillis* 5650 (MSC). CAMDEN CO.: Chew Road, *MacKenzie* 6912 (NY). CAPE MAY CO.: Cape May Court House, *Gillis* 5632 (MSC). CUMBERLAND CO.: Buena, *Gillis* 5642 (MSC). HUNTERDON CO.: Ellmaker Island, Raven Rock, near Stockton, *collector unknown* (MIN). MERCER CO.: between Princeton and Rocky Hill, roadside, *Gillis* 5089 (MSC). MIDDLESEX CO.: East Millstone, Hutcheson Memorial Forest, *Gillis* 3472 (MSC); Perth Amboy, *Gillis* 5387 (MSC). MONMOUTH CO.: Freehold, *MacKenzie* 7941 (NY). OCEAN CO.: Barnegat Pier, *MacKenzie* 2918 (GH); Island Beach State Park, dominant shrub for 10 miles, *Gillis* 2709 (MSC). SALEM CO.: Penns Grove, *Adams & Adams* 1890 (A, US). SOMERSET CO.: Hillsboro Twp., Sourland Mt., Neshanic-Zion Road, *collector unknown* (NDA). UNION CO.: Rahway, *Gillis* 5090 (MSC). WARREN CO.: Phillipsburg, *Tidestrom* 6009 (US). **New York.** BRONX CO.: Bedford Park, *Edmondson* 1420 (NY). DUCHESS CO.: Brush, *Gillis* 4065 (MSC). GREENE CO.: without definite locality, *Gillis* 3830 (MSC). MANHATTAN CO.: Van Courtlandt Park, *Hastings, s.n.* (NY). NASSAU CO.: Lawrence, *collector unknown,* (ND-G). RENNSELAER CO.: Troy, *Hall, s.n.* (F). RICHMOND CO.: Staten Island, *Dowell* 4641 (MIN). SUFFOLK CO.: Shelter Island, *Wells, s.n.* (MSC); 3 miles south of Montauk Point, *Gillis* 4924 (MSC). WESTCHESTER CO.: Shrub Oak, *Gillis* 4064. **North Carolina.** ALAMANCE CO.: 4.6 miles north of Union Ridge, *Ramseur & Hammond* 2552 (FSU). BRUNSWICK CO.: Long Beach, *Boyce* 1424 (NY). BUNCOMBE CO.: Biltmore, *Bartlett* 2905 (ARIZ, TEX). CAMDEN CO.: Elizabeth City, *Gillis* 3866 (MSC). CATAWBA CO.: east of Conover, *Gillis* 6053 (MSC). CURRITUCK CO.: Currituck Sound, *Randolph & Randolph* 599 (GH). DARE CO.: Pea Island, *Gillis* 4041 (MSC). DAVIE CO.: Farmington, *Gillis* 6066 (MSC). DURHAM CO.: Nelson, *Gillis* 4029 (MSC). FORSYTH CO.: Clemmons, *Gillis* 6072 (MSC). HALIFAX CO.: Enfield, *Ahles* 14917 (GH). HERTFORD CO.: Potecasi Creek, SE of Mapleton, *Ahles* 41517 (FSU). HOKE CO.: 0.2 mile NW of Hoke-Robeson Co. line, *Ahles* 29584 (FSU). MACON CO.: Topten, *Donahue* 257 (MSC). ORANGE CO.: Chapel Hill, *Gillis* 4028 (MSC). PERQUIMANS CO.: Hertford, *Gillis* 3868 (MSC). POLK CO.: Varyhans Gap, *Peattie* 1476 (F); Tryon, *Churchill, s.n.* (MO). SWAIN CO.: SW of Nantahala, *Donahue* 258 (MSC). WAKE CO.: Raleigh, *Hyams s.n.* (US). **Pennsylvania.** ADAMS CO.: East Berlin, *Gillis* 4902 (MSC);

BEDFORD CO.: New Baltimore, *Gillis* 5484 (MSC); 3.5 miles south of Centerville, *Westerfeld* 6568 (FSU). BUCKS CO.: Bowman's Hill, *Gillis* 3840 (MSC); Washington Crossing, *Gillis* 3836 (MSC). DAUPHIN CO.: Harrisburg, *Small, s.n.* (F). FRANKLIN CO.: Tuscarora Mountain, *Gillis* 5110 (MSC); MONTGOMERY CO.: Cold Point, *Adams & Adams* 1970 (A). MONTOUR CO.: Mausdale, *Adams* 5948 (OSC). NORTHAMPTON CO.: Easton, *Gillis* 4904 (MSC). PERRY CO.: Newport, *Adams & Adams* 3666 (A, GH); PHILADELPHIA CO.: Mermaid, *Adams & Adams* 1883 (A); SNYDER CO.: Selinsgrove, *Moldenke* 2459 (NY); YORK CO.: Dilsburg, *Gillis* 4903 (MSC). **Rhode Island.** BRISTOL CO.: Barrington, *Winslow, s.n.* (US). KENT CO.: West Warwick, *Gillis* 4103 (MSC). NEWPORT CO.: Newport, *Mearns* 233, 235, 236 (A, GH, BM, ND-G, NY, US). PROVIDENCE CO.: Grant's Mill, *Palmer* 43426 (MO, NY). WASHINGTON CO.: Wickford, *Williams, s.n.* (GH). **South Carolina.** AIKEN CO.: Graniteville, *Eggert, s.n.* (MO); ANDERSON CO.: Whitner Park, *Davis* 1710 (MIN, OSC); BAMBERG CO.: Denmark, *Palmer* 39863 (A, MO, NY). BERKELEY CO.: Pineville, *Godfrey & Tryon* 579 (GH, NY, US). FLORENCE CO.: Branch Swamp, *Bartlett* 2372 (MICH). LEXINGTON CO.: Batesburg, *MacGregor* 26 (US). OCONEE CO.: Clemson College, *House* 3103 (NY, US). RICHLAND CO.: north of Columbia along highway 21, *Gillis* 4570 (MSC). WOOD CO.: without definite locality, *Davis* 2041 (US). YORK CO.: Ebenezer, Branch Swamp, *Bartlett* 2373 (MICH, MSC). **Tennessee.** SEVIER CO.: Great Smoky Mountains National Park, 1/2 mile from Gatlinburg, *Gillis* 6541 (MSC). FRANKLIN CO.: Sherwood, *Eggert, s.n.* (MIN). HARDEMAN CO.: Bolivar, *Palmer* 17499 (A, MO, US). HENDERSON CO.: Natchez Trace State Park, *Donahue* 212 (MSC). KNOX CO.: Island Home Park, *Ainslie, s.n.* (KSC). **Texas.** HARRIS CO.: Houston Memorial Park, *Traverse* 18 (F, GH, SMU); MONTGOMERY CO.: Willis, *Dixon* 292 (F). WALKER CO.: Stubblefield Lake Recreation Area, *Donahue* 235 (MSC). **Vermont.** CHITTENDEN CO.: Charlotte, *Harsford, s.n.* (MIN). WINDHAM CO.: Westminster, *Gillis* 4083 (MSC). WINDSOR CO.: White River Jct., *Gillis* 4089 (MSC). **Virginia.** ARLINGTON CO.: Fort Myer, *Mearns* 103 (US). BEDFORD CO.: without definite locality, *Curtiss, s.n.* (GH). DINWIDDIE CO.: Burgess Station, *Fernald & Long* 9973 (GH, PH). FAIRFAX CO.: Great Falls, *Bartlett* 1785, 1779, 1787 (MICH, MSC). GREENE CO.: Bear Fence Mt., *Walker* 2951 (US). HANOVER CO.: Mechanicsville, *Adams & Wherry* 2216 (A). HENRICO CO.: Curles Neck Farm, *Fernald, Long & Smart* 5832 (GH, NY). ISLE OF WIGHT CO.: Rushmere, *Fernald & Long* 13066 (GH, MIN, PH); Carrollton, *Gillis* 4043 (MSC). NANSEMOND CO.: South Quay, *Fernald & Long, s.n.* (GH, PH). NORFOLK CO.: Ocean View, *Kearney* 1759 (US); Lambert's Point, *Kearney* 1026 (US). NORTHAMPTON CO.: Capeville, *Gillis* 3864 (MSC); Exmore, *Gillis* 3862 (MSC); PRINCE GEORGE CO.: Desputanta, *Fernald, Long & Smart* 5833 (GH, NY, PH, US). PRINCESS ANNE CO.: Virginia Beach, *Britton & Small, s.n.* (F, NY, US); SOUTHAMPTON CO.: Oak Grove School, *Fernald & Long* 8351 (GH, MO, PH). SURRY CO.: Chippokes,

Fernald & Long 13064 (GH, NY, PH, US); SUSSEX CO.: Huske, *Fernald & Long* 13067 (GH, PH, US); Jarratt, *Fernald & Long* 13381 (GH, PH, WIS); WARWICK CO.: Hampton, *Churchill, s.n.* (MIN, MO, WIS). WESTMORELAND CO.: Colonial Beach, *Tidestrom & Bartlett* 5962 (A, MO, US). YORK CO.: James River, *Killip* 40122 (US). **West Virginia.** HAMPSHIRE CO.: Capon Bridge, *Gillis* 5707 (MSC). KANAWHA CO.: Kanawha State Forest, *Donahue* 262 (MSC). MONONGALIA CO.: Morgantown, *Millspaugh* 146 (NY). RANDOLPH CO.: Huttonsville, *Donahue* 264 (MSC). UPSHUR CO.: Bucklin, *Pollack, s.n.* (US). WEBSTER CO.: Hacker Valley, *Smith* 1532 (F).

CANADA. **Nova Scotia.** QUEENS CO.: Port Mouton, *Jack* 3476 (A, F). SHELBURNE CO.: Welshtown (Birchtown) Lake, *Fernald & Long* 24094 (GH). YARMOUTH CO.: Gavelton, *Fernald & Long* 24098 (GH); Argyle Head, *Long & Linder* 21790 (GH); Yarmouth, *Pease & Long* 21785 (GH).

BERMUDA. Paget East, *Hughes, s.n.* (MSC). Tucker's Town, *Brown* 499 (NY). Boaz Island, *Brown & Britton* 1005 (NY).

BAHAMA ISLANDS. **Abaco.** Marsh Harbor, Great Abaco, *Brace* 1840 (NY); Great Abaco, 3 miles south of Treasure Cay, *Gillis* 6157 (MSC). **Andros.** North Andros, Staniard Creek, *Small & Carter* 8850 (NY). **Bimini.** South Bimini, without definite locality, *Howard & Howard* 10061 (NY, SMU). **Cat Cay:** North Cat Cay, without definite locality, *Millspaugh* 2336 (NY). **Grand Bahama.** Without definite locality. *Britton & Millspaugh* 2446 (NY); Russell Town near Freeport, *Gillis* (FTG). **New Providence.** Delaport, *Britton* 3416 (NY); Southwest shore of Lake Cunningham, *Gillis* 6074 (MSC).

This subspecies probably represents the form of poison-ivy which was first encountered by seventeenth century explorers and settlers in the New World. Early collections from North America, made in colonies close to the Atlantic Seaboard, were either of this taxon or, if found north of the 44th parallel, of *Toxicodendron rydbergii.* The designation of a type for *Rhus radicans L.* has presented a dilemma, because of the various specimens known to have been available to Linnaeus.

Linnaeus's first reference to poison-ivy was in the *Hortus Cliffortianus* (1738): *Rhus radicans foliis ternatis: foliolis petiolatis ovatis nudis integerrimis.*" Linnaeus based his early concepts of poison-ivy on the collections other than at Uppsala, such as that of Clfford's. The Clifford specimens are probably the ones upon which Linnaeus based most of his knowledge of poison-ivy. (These specimens, now at BM, are a flowering representative of *T. rydbergii*, and a sterile

branch of *T. radicans* subsp. *radicans.*) They undoubtedly represent Linnaeus's concept of poison-ivy until after the publication of the *Hortus Cliffortianus.* In 1751, however, Peter Kalm returned from his exploring and collecting adventures in North America, bringing with him many specimens which were incorporated into Linnaeus's personal herbarium. Among these was a form of poison-ivy, presumably from the vicinity of Philadelphia(Kalm, 1770), for which Linnaeus must have had some habit data, for he edited his diagnosis of *Rhus radicans* from the *Hort. Cliff.* in *Species Plantarum* (1753) by the insertion of the phrase "*caule radicante,*" thus suggesting that he had learned of its habit as a liana. The population represented in the Clifford Herbarium by the flowering specimen *(T. rydbergii)* has no aerial roots and did not climb. Although both the Clifford specimens (already familiar to Linnaeus), and the Kalm specimen (representing a phase of the plant new to Linnaeus), were all under consideration by him at the time of writing of the *Species Plantarum,* the Kalm specimen has been confirmed as the lectotype. It is the specimen which demonstrates the climbing habit, thus the added phrase in the Species Plantarum. The Clifford specimen, representing a non-climbing form of poison-ivy, must be excluded as a candidate for the nomenclatural type. Fernald alludes to the LINN specimen as being the type by publishing (1941) a photograph of it labeled "portion of type," but Brizicky (1963) formally designated it as the lectotype. If Linnaeus knew of the non-climbng habit of the Clifford specimen and any other departures from the characteristics represented in the Kalm specimen, he chose not to separate these plants nomenclaturally. This was finally done at the end of the nineteenth century when Rydberg (1900) published Small's name *Rhus rydbergii.*

The type material leaves much to be desired in the way of diagnostic characteristics. After study of the material in the Linnaean Herbarium, I have concluded that the Kalm specimen must represent the Atlantic Coastal population, corroborating the hint in Kalm's records that he collected it near Philadelphia. What has been most influential in

making this decision is the characteristic tufts of hairs in the main vein axils on the lower surface of the leaflets, a characteristic only of Oriental and Atlantic Coast forms. Had the specimen been a fruiting one, the pubescence of the exocarp would have solved the dilemma. Populations from the eastern coastal regions of the United States generally have entire leaflet margins, although not uncommonly with a single lobe or notch each leaflet (two on the terminal) as has the Linnaean specimen. The division of the terminal leaflet into inequilateral halves is a more subtle, although persistently accurate character, and is found in this specimen also. Complicating matters is the additional specimen in the Linnaean Herbarium (sheet 387.15) which has almost glabrous fruit. This specimen is anomalous as to the population which it can represent. It is therefore better to consider that Brizicky has chosen the appropriate specimen for nomenclatural typification.

Curiously enough, most taxonomists, even those who have worked extensively with the poison-ivy problem, have ignored typification of this species and the type subspecies. Many subspecies, varieties, and forms have been described, which all apply to the same taxon as the Linnaean specimen. This is due in part to the fact that the Kalm specimen was collected in flowering condition. Had it been a fruiting specimen with the fruit's characteristic trichomes on the exocarp, the publishing of such epithets as *microcarpon*, *malacotrichocarpum*, and *littoralis* (each used in several combinations) might have been precluded.

The fruits of subsp. *radicans* are generally smaller than the fruits of other subspecies of *Toxicodendron radicans*. This is especially true in populations which are found in Florida and southern Georgia. The small-fruited forms seem to demonstrate some geographical pattern, but otherwise do not differ from other populations of subsp. *radicans*, and therefore do not seem to warrant nomenclatural segregation. The various taxa using the epithet *microcarpon* or its orthographic derivatives are therefore treated in synonymy with subsp. *radicans*.

In regard to the type of *Rhus littoralis* Mearns, there are two sheets and a box of twigs and fruits comprising the type at US, one of the sheets containing a fruiting specimen and one a portion of the stem with abundant aerial roots. Presuming that these all represent a single specimen, thereby fulfilling the requirement of Art. 9 of the Code, these all represent the type specimen. A specimen labeled "isotype" is deposited at GH, but collected 11 days before the type (*Mearns* 232). Furthermore, US-403299 (*Mearns* 235) is probably an isotype. Mearns appears to have numbered each specimen with a separate collection number even though many may be part of the same gathering.

Because the name *Rhus radicans* var. *littoralis* has been applied (Deam, 1940) to populations which do not belong to this taxon, it seems appropriate to discuss the likely reason that this application was made. Some populations of poison-ivy in Indiana, especially from counties bordering the Ohio River, have fruits which are pubescent to a greater or lesser extent; they are, however, dissimilar in other respects to populations from the coastal regions which are truly *Toxicodendron radicans* subsp. *radicans*. This is also true for some populations in Oklahoma (which were named *T. aboriginum* by Greene, 1905). The epithet *littoralis* is misapplied; the populations of Indiana and Oklahoma should be *T. radicans* subsp. *negundo*.

In describing several new varieties and forms, Fernald (1941) described a number of taxa represented in southeastern Virginia. He did not until later (1950) indicate the reasons for his new taxa. He implied that forma *intercursa* (= "running between"), with its supposed pubescent leaf blades and glabrous petioles, was intermediate between forma *vulgaris*, which he said had both leaf surfaces and petioles glabrous, and f. *negundo*, which allegedly had both leaf surfaces and petioles pubescent. These characters in the populations in question, especially petiole pubescence, are highly variable.

We are able to typify *Toxicodendron glabrum* Mill. by Miller's reference to Dillenius's *Toxicodendron rectum foliis minoribus glabris* for which there is a specimen in the

Dillenian Herbarium; this specimen has been designated the lectotype. It was a cultivated specimen, grown in 1727 by Sherard. It is not surprising, its being a cultivated plant, that it is an atypical form of *T. radicans* subsp. *radicans* with very narrow leaflets and almost total lack of the characteristic tufts of hairs in the vein axils on the lower leaflet surface, conditions strongly suggestive of the possibility that the specimen is a juvenile. By reference to this Dillenian citation, *Rhus radicans lucidum* Aiton and *R. humilis* Salisbury[15] (as *R. humile*) can also thus be typified. Greene (1910) interpreted this plant as near his *T. rufescens* or *R. littoralis* Mearns. According to Britten (1900), *T. glabrum* Mill. "is made a synonym of *Rhus glabra* in Ind. Kew. The character 'foliis ternatis' is sufficient to show that this cannot be the case; since we have not Miller's specimens, but the figure which he quotes from Hort. Elth. represents *R. radicans*." *Toxicodendron glabrum* (L.) Kuntze is most likely *R. glabra* L. since Kuntze virtually obliterated *Rhus* by wholesale transfers to *Toxicodendron*.

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[15]Dillenius (1732) intended that his *Toxicodendron amplexicaule, foliis minoribus glabra* be different from *Toxicodendron rectum, foliis minoribus glabris*. Linnaeus must have agreed, since he quoted the former as synonymous with his variety β, and the latter with his variety γ. The descriptions by Dillenius indicate that he thought *Toxicodendron amplexicaule*. . . . was a climber, and *Toxicodendron rectum* . . . was not. His illustration of *Toxicodendron rectum*. . . , however, appears to be of the climber *Toxicodendron radicans* subsp. *radicans* as herein treated. Moreover, the specimen at the Sherard Herbarium which Dillenius saw demonstrates *Toxicodendron rectum* . . . to be *T. radicans* subsp. *radicans*, despite a written description to the contrary. This becomes of importance when one tries to determine what Salisbury meant by his *Rhus scandens* and *R. humile*.

Rhus humilis must refer to *T. radicans* subsp. *radicans* also, although typified by another specimen (the one at Sherard), even though its description more nearly fits *T. rydbergii* than *T. radicans*. Because a specimen can be found for at least one of these polynomials of Dillenius, we can attribute this one (*Toxicodendron rectum* . . .) to *T. radicans* subsp. *radicans*. Where we have a description, an illustration, and a specimen, the specimen must be granted precedence over all else in typifying, even though it is not correctly defined by the illustration or description. *Rhus scandens*, because of its reference to *Rhus radicans* L., must also be *T. radicans* subsp. *radicans*.

In other words, Miller meant a poison-ivy plant by his use of *Toxicodendron glabrum*; Kuntze did not.

In naming *Rhus blodgettii*, Kearney (1894) described clusters of flowers, but later in the paper admitted that flowers were not seen. His specimen is fairly typical *Toxicodendron radicans* subsp. *radicans*, except for the absence of pubescence on the fruits, but southern Florida populations often have glabrous fruits. Barkley annotated the lectotype as follows:

"Dr. Kearney in the description of the type says, 'The single specimen which I have seen was collected by Blodgett at Key West, Florida. It is in the Torrey Herbarium.' As this is the only Blodgett *Rhus* in the Torrey Herbarium and it fits the description, it is probable that it represents the TYPE."

In regard to *Toxicodendron goniocarpum* Greene, two specimens at US fit Greene's description of the type. I have chosen the fruiting specimen, *McCulloch* 45 (sheet 440443) as the lectotype. *McCulloch* 46 (sheet 440444) is a probable isotype (presumably McCulloch numbered specimens rather than collections). Greene probably had both specimens under consideration since he describes the "rooting freely" of the sterile specimen and the nature of the fruits of the second specimen.

Many specimens of this subspecies are teratological forms, in which the inflorescence proliferates primary and secondary bracts in place of fertile flowers. As I noted earlier (Gillis, 1960), "In these aborted flowers, the bracts grow to several times their normal length (up to 1.4 cm) and were arranged like the flowers, occasionally opposite and occasionally alternate." This monstrosity has been seen expressed in most taxa of poison-ivy and the poison-oaks, as well as in other *Toxicodendron* and *Rhus* species. Whether this is a response to a virus, insect damage, or some other environmental factor is unknown. It is not genetic in that it does not appear in the same population year after year. It does, however, occur with greatest frequency in *T. radicans* subsp. *radicans*, most especially in the Middle Atlantic and New England States.

One item of periodicity should be noted here. This subspecies is the only member of the poison-ivy complex which digresses from being strictly deciduous. Populations in South Florida retain their leaves until a flush of growth produces new ones, about the time of flowering in February and March. Thus, the plant is never without leaves. Also in South Florida, this subspecies has been seen growing as an epiphyte, rooted not in the ground, but in the old leaf bases of palms in the Everglades.

This subspecies is the most abundant of all poison-ivy taxa, especially in New Jersey, southern New York, and Long Island. Along a stretch of road between the Delaware River and Princeton, New Jersey, poison-ivy forms a roadside carpet for about 15 miles, covering every patch of ground not occupied by some protruding plant, a house, or an intersection, and climbs every tree on both sides of the road! At Island Beach State Park, New Jersey, in the zone protected from salt spray behind the foredunes, poison-ivy forms a dense, shrubby mat, seldom interrupted, between the foredune and the roadway for a distance of 10 miles, about 50-75 meters in breadth. The subspecies becomes less common toward the southern edge of its range, possibly being less able to compete with the more vigorous vines and shrubs in warmer climes.

This subspecies has greatest affinities with Asiatic subspp. *orientale* and *hispidum*. All populations have pubescent fruits, entire leaflet margins (with, at most, only a single notch on each abaxial edge), a characteristic tuft of red-brown or hyaline hairs in the major vein axils on the lower surface of the leaflets, and ovate or elliptic leaflets with acute to acuminate apices. Subspecies *radicans*, however, generally has truncate or obtuse terminal leaflet bases, the broadest portion of the ovate terminal leaflet below center, the tufts of hairs in vein axils generally hyaline or straw-colored rather than red-brown, and small, globose fruits. It is possible that these three subspecies represent disjunction of a taxon that was once contiguous through Eastern Asia and North America.

This subspecies appears to form intergrades with other

taxa where their ranges come into contact. Putative hybrids, intermediate between subsp. *radicans* and *T. rydbergii,* are known from the Berkshire Mountains of western Massachusetts and elsewhere in southern New England. The plant also appears to form hybrids with subsp. *pubens* in Louisiana, Arkansas, and Texas, and with subsp. *negundo* along the Allegheny Ridge (especially Tuscarora Mountain) in Pennsylvania and the Blue Ridge in Virginia, West Virginia, and Maryland. (See discussion under Hybrids, Crosses, and Intergrades; citation of presumed intermediate forms may also be found under that heading.)

Toxicodendron radicans subsp. *radicans* has a broad ecological amplitude. It is most abundant on sand dunes, along fencerows, in floodplain forests, and old fields. It manages to exist marginally as drainage becomes extreme, either with high water table or excessive drainage, such as borders of peat bogs or salt marshes, wet muck, on podzols, or on shallow lithosols. In Nova Scotia, however, one may find it, in addition to sites mentioned above, on gravelly barrens. In the Bahama Islands, it grows in pinelands or hammocks on rocky limestone. In the Florida Everglades, it inhabits leaf mold on potholed limestone.

This taxon has broad community relationships. In its northern reaches, it is closely affiliated with the beech-maple forest and what has evolved from the oak-chestnut woods following the demise of the chestnut. Along the Atlantic and Gulf Coastal Plains, it is often abundant in loblolly pine woods, especially where there is little or no oak present. Farther south, on the Coastal Plain, it is found frequently in liveoak *(Quercus virginiana)* forests and is reported as forming an association with *Persea* in northern Florida (herbarium notes). Along the Gulf Coastal Plain, it is common in southern hardwood forests of *Liquidambar styraciflua, Nyssa aquatica, Quercus virginiana, Fraxinus spp.,* and *Acer rubrum.*

On sand dunes it is abundant enough to form an association of its own behind the foredunes where it receives only moderate salt spray (I have observed that a good 2-day northeaster in the Middle Atlantic States and New England

is sufficient to defoliate an entire population in a sand dune association). On the dunes, its frequent associates are *Parthenocissus quinquefolia, Myrica pensylvanica,* and *Smilacina racemosa.*

In the Bahama Islands, its chief habitats are relatively dry (no standing water) mangrove swamps associated with *Rhizophora mangle, Erithalis fruticosa, Blechnum serrulatum, Achrostichum aureum, Bumelia salicifolia, Chrysobalanus icaco,* and *Sabal palmetto.* On some sites, in relatively undisturbed communities, it favors the "blacklands": woods of fairly dense *Pinus caribaea* often associated with *Bumelia, Pteridium aquilinum* var. *caudatum, Duranta repens, Trema lamarckiana,* and *Ilex krugiana.* On New Providence, it is reported from the more open pinelands called "whitelands." At this extreme limit of its range, it appears to compete poorly with other shrubs and vines, being absent from most thickets. I have searched for it on some of the eastern islands in the Bahama Archipelago (San Salvador, Rum Cay, Cat Island) to no avail.

Throughout its range, subsp. *radicans,* as well as subspp. *negundo* and *pubens,* are constantly associated with *Parthenocissus quinquefolia, Ulmus spp., Fraxinus spp.,* and often with *Clematis spp.* and *Ampelopsis arborea.*

4b. **Toxicodendron radicans** subsp. **orientale** (Greene) Gillis, comb. nov. Fig. 35.

Toxicodendron orientale Greene, Leafl. Bot. Observ. Crit. 1: 127. 1905. *Rhus orientalis* (Greene) Schneider, Illust. Handb. Laubholzk. 2: 151. 1912. Type: *Maximowicz, s.n.* Hakodate, Hokkaido, Japan. 1862. (US-19948, not US-19548 as cited by Greene, 1905, holotype; G-DC, isotype).

Rhus ambigua Lavallée, Arbor. Segrez., p. 54. 1877. Type: unknown, probably a living plant.

Rhus rishiriensis Nakai, Bot. Mag. (Tokyo) 36: 67. 1922. *Rhus ambigua* f. *rishiriensis* (Nakai) Hara, Enum. Sperm. Jap., Part 3, p. 65. 1954. Type: *H. Koidzumi, s.n.* Japan, Rishiri To, Hokkaido, Oshidomari Mts., growing with *Abies sachalinensis.* (TI, holotype).

Fig. 35. *Toxicondendron-radicans* subsp. *orientale*. Type of *Toxicodendron orientale* Greene, Maximowicz.

Leaves bearing tufts of hairs in vein axils on lower surface, generally light-colored to red-brown. Terminal leaflet blade 1.2-1.7 times as long as broad, widest part generally at the middle or above middle, 5-20 cm long, 3-12 cm wide; cuneate at base; petiolule 0.5-3.0 cm long. Petiole 1.5-11.0 cm long. Fruits flattened, obliquely deltoid, 5-6.5 mm broad, short hairy or papillose.

Distribution: Japan, U.S.S.R. (Kurile Islands, Sakhalin). Common name: tsuta-urushi. Fig. 36.

Fig. 36. Distribution of *Toxicodendron radicans* subsp. *orientale*.

Representative specimens. JAPAN: **Hokkaido.** HIDAKA PROV.: Shoya, Horoizumi-gun, *Tokubuchi, s.n.* (SAP, TI). IBURI PROV.: Noboribetsu on road to Noboribetsu Hot Spring, *Gillis* 4717 (MSC); Mt. Tarumai, *Ito, s.n.* (SAP). ISHIKARI PROV.: Mt. Teine, *Yanagissawa, s.n.* (SAP); Sapparo, *Tokubuchi, s.n.* (GH); Sapporo, *Sugimoto, s.n.* (MSC, TI); Lake Shikotsu, *Gillis* 4743 (MSC); Usakuma National Forest, *Gillis* 4760 (MSC); Asahigawa City, Kamikawa, *Miyabe, s.n.* (SAP). KITAMI PROV.: Shiretoko Peninsula, *Ito* 376 (SAP); Shakubetsu, *collector unknown* (TI); Shari, *Kanai, s.n.* (TI); Rishiri Islands, Oshidomari, *Suzuki, Komiga, & Shirahama, s.n.* (SAP); Rishiri Islands, Oniwaki, *Shirahma, s.n.* (SAP). OSHIMA PROV.: Hakodate, *Albrecht, s.n.* (GH, MO, NY); *Maximowicz, s.n.* (GH, NY, US); Yoshioka-mura, *Miyabe & Tashiro, s.n.* (SAP); Esashi, *Sasayama, Miyabe, & Tashiro, s.n.* (SAP). SHIRIBESHI PROV.: along the Tomarikawa, Mt. Shakotan, Shimamaki-bun, *Misumi & Igarashi, s.n.* (SAP); Okuskiri Islands, *collector unknown* (SAP). TESHIO PROV.: Teshio, *Tsujii & Kozuka, s.n.* (MSC, SAP). **Honshu.** AOMORI PREF.: Mutsui Horosaki, *Sakurai, s.n.* (A); Mt. Hakkoda, *collector unknown* (TI). CHIBA PREF.: Awa-Amatsu, 1.3 km. SW of Kameyama, *Gillis* 4678 (MSC); Chiba, *Kanai, s.n.* (TI). ESHIGO PREF.: Mt. of 5 Peaks, *collector unknown* (TI). FUKUI PREF.: Echizen, Tsuruga, *Kitamura & Murata* 2042 (MSC). FUKUSHIMA PREF.: Kashi Hot Spring, *Kanai, s.n.* (TI); Jokogi, *Muramatu, s.n.* (TI): Mt. Bandai, *Koyama, s.n.* (MSC). GIFU PREF. Nakatsugawa, *Kanai, s.n.* (TI); Kisogoe Pass, *Kanai, s.n.* (TI); Mt. Ibuki, *Kanai, s.n.* (TI). GUMMA PREF.: Mt. Tanigawa, *Takeushi, s.n.* (TI); Mt. Hodaka, Kanto District, *Kanai, s.n.* (TI); Oze, *Nishida, s.n.* (TI); Usui Pass, *Kanai, s.n.* (TI). HIROSHIMA PREF.: Mt. Aza, *Kanai, s.n.* (TI). IWATE PREF.: Moichi, *Kanai, s.n.* (TI); KANAGAWA PREF.: Mt. Hakone, *Kanai, s.n.* (TI). Hata, *Bisset* 3890 (E). MIYAGI PREF.: Matushima, *Faurie* 484 (A); Sendai, *Ogina, s.n.* (TI); Okunikawa, *collector unknown* (TI). NAGANO PREF.: Shimajimadam, *Momose, s.n.* (MSC); Kuzu, Omachi, *collector unknown* (TI); Nagawado, *Kanai, s.n.* (TI); Mt. Hachibuse, *collector unknown* (TI); NAGASAKI PREF.: Mt. Yatate, Tsushima Island, *Yabe, s.n.* (TI); Irikan, *Ohki, s.n.* (TI). NARA PREF.: Mt. Odaigahara, *Ohwi, s.n.* (WIS). Niigata Pref.: Mt. Azogi, Sado Island, *Kanai, s.n.* (TI); Niigata, *Yamazaki, s.n.* (TI, US). OKAYAMA PREF.: *Okayama, Uno, s.n.* (NY). SHIGA PREF.: near Kyoto, *collector unknown* (TI); Shiga Highland, *Kanai, s.n.* (TI); Makino, *Kanai, s.n.* (TI). SHIZUOKA PREF.: Mt. Amagi. Izu Peninsula, *collector unknown* (TI); Mt. Daruma, Izu Peninsula, *Kanai*, s.*n.* (TI); Mt. Ashitaka, *Kanai* 5847 (TI); Mt. Senmai, *collector unknown*, (TI); Gotemba, *Hisanchi, s.n.* (MSC, TI). TOCHIGI PREF.: Chuzenji, *Juenberg, s.n.* (A); Nikko, *Kanai* 4030 (TI); Nikko, *Gillis* 4788 (MSC); Chugiyi, *Gillis* 4781 (MSC); Sampeitoge Pass, *Mishida, s.n.* (MSC). TOKYO PREF.: Mitake, *Kanai* 163 (TI); Motohachioji, *Kanai, s.n.* (TI); Asakawa, *Kanai* 3221 (TI); Okutama, *Kanai* 4388 (TI); University Botanical Garden, *Gillis* 4625 (MSC).

WAKAYAMA PREF.: Kii, *Murata* 15138 (MSC); Mt. Koya, *Uno, s.n.* (A). YAMAGATA PREF.: Asahimachi, *Kanai, s.n.* (TI). YAMAGUCHI PREF.: collector and exact locality unknown (TI); YAMANASHI PREF.: Asagoduta, Fuji, *Hayata, s.n.* (TI); Mt. Kenashi, foot of Fuji, *Kanai, s.n.* (TI); Mt. Riugatake, foot of Fuji, *Kanai, s.n.* (TI); Aokihara, *Hayata, s.n.* (MSC). PREFECTURE UNCERTAIN: Lake Chuging, *Wilson* 6876 (A, BM). Ugosakai, *Muramatsu, s.n.* (TI); foot of Mt. Nabekamudi, *collector unknown* (TI). Mt. Azima, *collector unknown* (A, TI). **Kyushu.** FUKUOKA PREF.: Takosara, *Takeda, s.n.* (E). KAGOSHIMA PREF.: Mt. Kirishima, *Wilson, s.n.* (A). KUMAMOTO PREF.: Mt. Asozu, *Kanai, s.n.* (TI); Tuabye Aso-san, *Maximowicz, s.n.* (BM). **Shikoku.** ECHIME PREF.: Mt. Dogo, *Satonii,* s.n. (TI); Uagima, *collector unknown* (TI). KOCHI PREF.: Nanogawa, *collector unknown* (TI); Nanogawa, *Watanabe, s.n.* (GH).

UNION OF SOVIET SOCIALIST REPUBLICS. **Kurile Islands.** Kunashir, Rebansa, *Shisahama & Takehashi, s.n.* (SAP); Kaikaramur, *Tatewaki, s.n.* (SAP); locality unknown, *Vorobjov* 92 (LE); Kinakai, *Pobedimova, s.n.* (MSC). Shakotan, Mt. Shakotan, *Ohwi* 526 (SAP). Sikotan, Sikotan-yama, *Vorobjov, s.n.* (MSC). **Sakhalin:** South Sakhalin Preserve, Nevelsky Region Kuznepovo, *Kravchenko* 49 (LE); locality uncertain, *Glehn, s.n.* (LE).

In naming a Maximowicz collection from Hakodate, Greene (1905) expressed the idea that his *Toxicodendron orientale* was sufficiently different from "any and all New World species that it forms a fair subgenus." The type has both flowering and fruiting stems, but suggests two inaccuracies in Greene's description. He indicated that the Japanese poison-ivy differs from North American poison-ivy by its petals not being "nervose and epicarp thinner . . ." These characters are, however, not borne out on the type specimen.

The first poison-ivy from eastern Asia with which one might be concerned nomenclaturally was described as *Rhus ambiqua* Lavallée, a nomen nudum. Dippel (1892) supplied the diagnosis. The name was used in connection with *Ampelopsis japonica,* a supposed synonym. Presumably Lavallée studied a living plant in the arboretum and therefore the name cannot be typified. Because the description is so brief, the name is frequently — and erroneously — attributed to Dippel (1892) whose description is more detailed. Masamune (1934) erroneously equated this name with *Rhus succedanea* var. *japonica* Engl. in DC. For

those who would recognize this taxon as a species of *Rhus*, the combination *Rhus ambigua* may not be used in any case since it was first published by Unger (1849) for an Eocene fossil of Italy, a plant not similar to the one under consideration here, but rather of the genus *Zanthoxylum* of later authors (Edwards and Wonnacott, 1935).

Nakai (1916b) felt that the poison-ivy called *Rhus toxicodendron* by Miquel (1865, and often attributed to Miquel as author of the binomial in Japanese literature) and *Rhus toxicodendron* var. *vulgaris* (sensu Engler, 1883) should be *R. ambigua* Lav. In his opinion, *R. orientalis* or *Toxicodendron orientale* should be reserved for Chinese or Hokkaido poison-ivy (Nakai, 1916b and Tanaka, 1916).[16] Nakai *(ibid.)* went on to say that Japanese poison-ivy was not poisonous, had larger flowers, more brown trichomes in the vein axils, and more nearly entire leaflet margins in comparison to American poison-ivy. His concept of *R. toxicodendron* was essentially that of Linnaeus, and therefore he felt that the binomial could not be used for any of the climbing forms in Japan.[17]

Hara (1939) compared Chinese and Japanese poison-ivy and arrived at the conclusion that they are the same species. He recognized that fruit pubescence is a critical character, but pointed out that this feature is variable even among specimens collected in the same area. He indicated that Chinese specimens are occasionally found to be nearly glabrous. It is likely that he was examining immature fruits when he made this observation, for the mature fruits are hispid in all Chinese poison-ivy specimens I have seen. Although Hara did not believe that the narrowness of the leaflets could be used to separate the two taxa, I feel that the ratio of length-to-width of the terminal leaflet is of taxonomic significance, and not narrowness (i.e., width)

[16]Schneider (1901) suggested that *Ampelopsis orientalis* Planch. in DC. is synonymous with *R. orientalis*, but this plant is most likely *Parthenocissus tricuspidata*.

[17]The common name of Japanese poison-ivy, tsuta-urushi ("climbing urushi") attests to the fact that the plant is a liana member of the lacquer tree group.

alone. This ratio is reasonably uniform within each of the two populations and therefore of importance in separating the two. The terminal leaflet in the Japanese populations is always less than twice as long as broad (1.2-1.7), whereas the Chinese populations are characterized by terminal leaflets closely approaching a length twice the breadth (1.9-2.0 times). The more subtle difference of a cuneate leaflet base in Japanese forms as opposed to an attenuate base in Chinese forms is less useful, but nevertheless seems to be a consistent character.

Nakai (1922) described a new species of poison-ivy from northern Hokkaido and the Rishiri Islands which he called *Rhus rishiriensis* (tachii-tsuta-urushi). Hara (1954) reduced this species to a form: *Rhus ambigua* f. *rishiriensis.* Koidzumi (1924) described its habitat as being the conifer forest of the Oshidomari Mountains of Rishiri To at 1050 meters. The taxon's only distinguishing character is that it does not appear to be scandent. Whereas the habit is generally considered to be reliable in poison-ivy taxonomy, in this case it is considered suspect. At the moment there seems to be little to verify its restricted growth on genetic grounds. The holotype (at TI) is indistinguishable from all other Japanese poison-ivies. It is most likely not cognate to *Toxicodendron rydbergii* of North America which, like its Japanese counterpart, does not climb and curiously similarly, does not grow south of the 44th parallel of latitude (Gillis, 1962). Forma *rishiriensis* appears impossible to characterize outside of the field, has not been proven to be a non-climbing plant at all times, and is inadequately collected. For the present it must be regarded as an ecological form from the windswept insular areas of northern Japan and far eastern U.S.S.R., not to be recognized nomenclaturally.

Toxicodendron radicans subsp. *orientale* grows in dense forests in Japan where it apparently sprouted when the forest was young, simply growing up with the forest. Reproduction within the forest is probably mostly restricted to individuals with some foliage in good light situations. From central Japan northward, it is often found in fir

forests. It is far less of a weedy species than its North American counterparts. Rather, it is a denizen of forest communities of the hills and mountains. Where there has been disturbance, such as a road cut, it becomes more abundant.

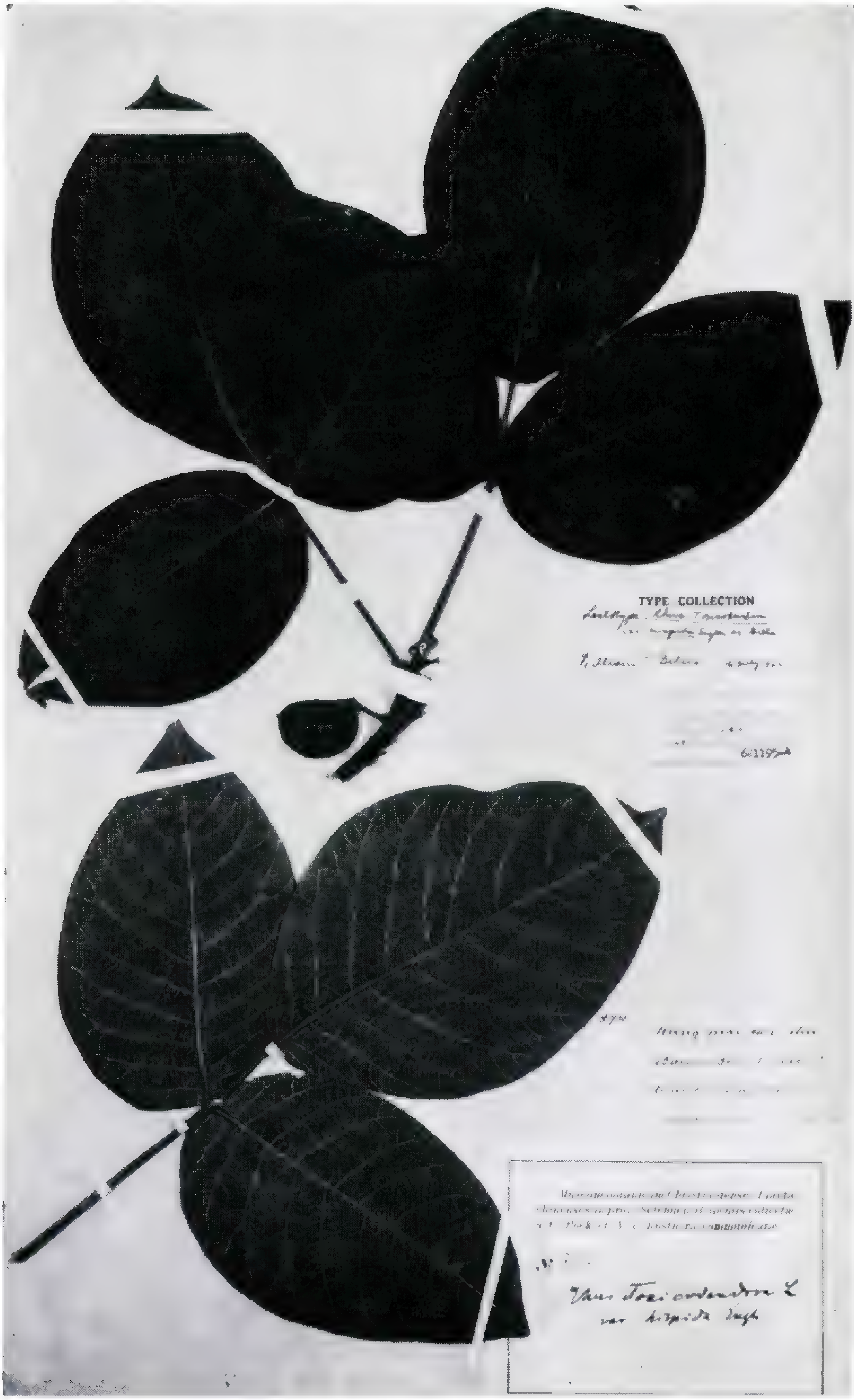
In northern Japan and the Kuriles, it is common in the forests of *Picea jesoensis* and *Abies sachalinensis* along with another liana, *Actinidia kolomikta.* In central Honshu where *Chosenia bracteosa* forms large forests, it is also a common woody climber (Tatewaki, 1950). Elsewhere in Japan, it is found in the pine-fir-redwood woods *(Pinus densiflora, P. thunbergii, Abies sachalinensis, Cryptomeria japonica).* In addition, Tatewaki (1958) has reported it as a typical inhabitant of the associations characterized by either *Aesculus turbinata, Fagus crenata, Pterocarya rhoifolia, Cercidophyllum japonicum, Acer mono,* or *Quercus crispula.* Its chief associates in most of these associations are also vines: *Vitis coignetiae, Hydrangea petiolaris, Actinidia arguta,* and *Schizophragma hydrangeoides* primarily, and secondarily *Celastrus orbiculatus* var. *papillosus, Schisandra chinensis,* and *Euonymus fortunei.* In the woods of the Boso Peninsula highlands (Chiba Pref.) the most common trees of the forests in which *T. radicans* subsp. *orientale* grows are *Quercus serrata, Castanea crenata, Lithocarpus edulis, Abies firma,* and *Pinus thunbergii.*

4c. **Toxicodendron radicans** subsp. **hispidum** (Engler in Diels) Gillis, comb. nov. Fig. 37.

Rhus toxicodendron var. *hispida* Engler in Diels, Bot. Jahrb. Supt. 29: 433. 1900. Type: *C. Bock and A. V. Rosthorn* 874. "Bamm (sic) 30′, 1″ circ., Wald. Lung mo-ai. Nanch'uan, China (Szechuan), 11 Sept. 1891." (O, lectotype).

Rhus intermedia Hayata, J. Coll. Sci. Imp. Univ. Tokyo 23 (art. 19): 73. 1908. Type: *T. Kawakami and U. Mori* 2024. Taiwan, Nantou County, Mt. Morrison, 7500 feet elevation, (TI, lectotype).

Widest part of the terminal leaflet blade generally at the middle or above the middle, nearly twice as long as broad,


TYPE COLLECTION

attenuate at the base, 6-20 cm long, 4-9 cm wide; petiole 3-11 cm long, terminal petiolule 0.3-3 cm long; tufts of hairs in vein axils below light-colored to red-brown. Fruits flattened, obliquely deltoid, 5-6.5 mm broad, hispid with hairs nearly 1 mm long.

Distribution: Western and central China and Taiwan. Common name: Taiwan tsuta-urushi. Fig. 38.

Representative specimens. PEOPLES REPUBLIC OF CHINA: **Hupeh.** Fang Hsien, *Wilson* 284. (A, E, GH, US). Changyang, *Wilson* 1128 (A, E, NY, US). Patung District, Ichang, *Henry* 4861 (K, NY), Locality unknown, *Henry* 6448 (A, E, BM, GH, MSC, US). **Sikang.** Huping, Paohing, *Wilson* 4647 (A). **Szechuan.** Nanchuan, *Bock & von Rosthorn* 874 (O); *Fang* 895 (A, E, MSC); *Hwang* 48 (A). Mt. Wa, *Wilson* 284a (A). Tachienlu, *Pratt, s.n.* (K). Cheng-Tu Plain,

Fig. 38. Distribution of *Toxicodendron radicans* subsp. *hispidum.*

Fig. 37. *Toxicodendron radicans* subsp. *hispidum.* Lectotype of *Rhus toxicodendron* var. *hispida* Engel. ex Diels, *Bock & Rosthorn* **874.**

Wang 22065 (GH). **Yunnan.** Liang-shan I'cho, *Tsai* 51280 (A). **Locality unknown.** *Henry* 2005 (K).

REPUBLIC OF CHINA (TAIWAN). **Chiayi Co.:** Mt. Arisan (also spelled Alishan), *collector unknown* (TAI); *Wilson* 10804 (US). *Linsley-Gressitt* 132 (BM, NY, U); *Hayata* (MSC); *Liu, Liao, Kuo* 2021 (MSC). **Ilan Co.:** Mt. Oobi, *collector unknown* (TAI). Mt. Bombon, *Eizi, s.n.* (TI). **Nantou Co.:** Saramao, *Eizi* 224 (TI); Mt. Taiheizan, *Suzuki, s.n.* (UC). **Taichung Co.:** Pai-koo-shan, *collector unknown* (TAI); Sing San, *Liu, Liao, Kuo, s.n.* (MSC). **Taipei Co.:** Taikokusyu, *collector unknown* (TAI); Taitung, Pa-Hsien-shan, *collector unknown* (TAI). **Locality unknown:** *Niitaka* (TAI).

A type was not designated by Engler for *Rhus Toxicodendron* var. *hispida,* although several specimens were cited in the original description. These were all destroyed by the 1943 bombing of the Berlin Herbarium. The only known extant duplicate of any of the cited specimens is the one at Oslo, hereby designated a lectotype.

Poison-ivy in Taiwan was named *R. intermedia* by Hayata (1908), who thought it was intermediate between sect. *Trichocarpae* and sect. *Venenata* of the genus *Rhus* (sensu Engler), due to the resemblance of the bristly trichomes of the Taiwan poison-ivy fruits to those of *Toxicodendron trichocarpum* (Miq.) Kuntze of Engler's sect. *Trichocarpae.* Even those who would retain this taxon as a species segregate of *Rhus* cannot use *Rhus intermedia* since this combination has been antedated by *Rhus intermedia* Ettingshausen (1888) for a Miocene fossil of Styria, Austria, a plant not conspecific with the taxon under consideration here.

In China poison-ivy is known from the central and western mountains, bordering on the Yunnan and Kweichow Plateaus and the foothills of the Tibetan Plateau in the provinces of Szechuan, Hupeh, Sikang, Kweichow, and Yunnan. There is a hiatus in the distribution of Chinese poison-ivy between these western mountains and the highlands of Taiwan, with none known in the intervening hills and plains. As Li (1963) has noted, there are phytogeographic links between the mountains of Taiwan and those of central and western China. In Taiwan, the plant is found growing on the Paleozoic slates of the central mountains.[18]

[18]Attempts on the part of the writer to study the poison-ivy com-

The ripe drupes of *Toxicodendron radicans* subsp. ***hispidum*** possess striking hispid hairs, often nearly 1 mm in total length, the longest fruit hairs in the genus. *Toxicodendron radicans* subsp. *orientale* has fruit with far shorter trichomes, often no longer than those of fruits of eastern North American taxa. On occasion, the fruits are papillose, rather than pubescent. As mentioned elsewhere, the papillose condition is interpreted as a form of incipient pubescence, the papillae being evaginated or reduced hairs. More than likely, mature fruits will be pubescent. The tufts of hairs in the vein axils on the lower surface are red-brown in about 60% of the specimens examined, hyaline or straw-colored in the remainder.

The closest relative of this subspecies is *Toxicodendron radicans* subsp. *orientale* of the Japanese Archipelago, which was probably derived from it. The three foregoing taxa, *T. radicans* subspp. *radicans*, *orientale*, and *hispidum*, are very similar morphologically, almost enough to form a separate cluster of taxa from all the other subspecies. All these plants have pubescent fruits, entire leaflet margins (with at most a single notch on each abaxial edge), the characteristic tufts of hairs that are red-brown or hyaline in the major vein axils on the lower surface of the leaflet, and ovate or elliptic leaflets with acute or acuminate apices.

They differ, however, by several reliable characters. The North American taxon has truncate or obtuse terminal leaflet bases; the broadest portion of the terminal leaflet is below center making the leaflet ovate; the tufts of hairs in the vein axils are generally hyaline or straw-colored rather than red-brown; the fruits are globose, 3-5 mm

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plex in China have been frustrated by the current political feud between the United States and the Peoples Republic of China. Correspondence, both in English and in Chinese, has been sent to the several botanical gardens and herbaria in China listed in Index Herbariorum (Lanjouw and Stafleu, 1964), all to no avail. A professor of biology at Nanking University was willing, but unable, to be of help. Even intercession on my behalf by journalist Edgar Snow with Premier Chou En-Lai yielded no specimens nor information. Because of these political difficulties, no specimens from any herbarium in the Peoples Republic of China were examined.

broad. The two Asiatic subspecies, on the other hand, have attenuate or cuneate terminal leaflet bases; the broadest portion of the elliptic or obovate terminal leaflet is above the mid-point; the flattened fruits are often obliquely deltoid as in the fruits of other *Toxicodendron* species in the Far East; the fruits are 5-6 mm broad; and the hairs in the vein axils are generally red-brown. The leaflets are generally smaller in subsp. *radicans* than those in the Oriental subspecies, although there is considerable overlap in size.

4d. **Toxicodendron radicans** subsp. **pubens** (Engelm. ex Watson) Gillis, comb. nov.

Rhus toxicodendron var. *pubens* Engelm. ex Watson, Bibliog. Index, p. 185. 1878. *Rhus radicans* var. *pubens* (Enge'm. ex Watson) Fernald, Rhodora 43: 596. 1941. Type: *F. Lindheimer* 247. High in thickets, not climbing, fl. odorous. New Braunfels, Comal Co., Texas. August 1846. (GH, lectotype; MO-1773730, MO-1773731, US-19858, isotypes).

Rhus toxicodendron var. *multifolia* Vines, Trans. Texas Acad. Sci. 26: 75. 1943. Type: *Robert A. Vines* B-3092. Bray's Bayou, Houston, Harris Co., Texas. 50 feet. July 1939. (SMU, holotype; MSC-190169, isotype).

Vine or shrub with aerial roots. Leaflet blade ovate, serrate, notched, or occasionally with one lobe on each edge; scabrous or rarely glabrous on the upper surface, often with a line of minute, curly hairs on the midrib, densely strigose, hirsute, or velutinous on the lower surface, velvety to the touch; without tufts of hairs concentrated in the vein axils. Terminal leaflet 3-20 cm long, 3-11 cm wide, acuminate; petiole 2-13 cm long, hispid, villous, or tomentose; terminal petiolule 0.3-5.0 cm long; veins on lower surface light in color, usually prominent and raised above the surface. Fruits glabrous, often glaucescent, rarely with incipient papillae or hairs, 3.0-4.5 mm broad.

Distribution: Former Eocene Embayment region of

Fig. 39. Distribution of *Toxicodendron radicans* subsp. *pubens* and subsp. *verrucosum*.

Lower Mississippi Valley west to East Texas, states of Mississippi, Louisiana, Arkansas, Missouri, Texas, southeastern Kansas. Fig. 39.

Representative specimens. UNITED STATES: **Arkansas.** ARKANSAS CO.: Arkansas Post, *Demaree* 21046 (MO, NY, SMU); St. Charles, White River National Wildlife Refuge, *Demaree* 48889 (MSC). CHICOT CO.: along US-82 adjacent to Ditch Bayou, *Gillis* 5939 (MSC). CRITTENDEN CO.: West Memphis, *Demaree* 11118 (GH). DREW CO.: Bayou Bartholomew, Tillar, *Demaree* 14665 (MIL, MIN, NY, SMU). FAULKNER CO.: Conway, *Moore, s.n.* (MSC). GARLAND CO.: Hot Springs National Park, Thousand Dripping Springs, *Demaree* 45564 (MSC). HEMPSTEAD CO.: Fulton, *Demaree* 42707 (SMU). HENRY CO.: Windsor Spring, *Hitchcock, s.n.* (MO). HOWARD CO.: Ouachita Region, Baker Springs near Umpire, *Demaree* 55705 (MSC). LEE CO.: La Grange,

Mariana-Helena Recreational Area, *Demaree* 47848 (MSC). LOGAN CO.: base of Magazine Mountain, near Blue Mountain, *Palmer* 24810 (A). MARION CO.: Yellville, *Demaree* 47910 (MSC). MONTGOMERY CO.: Mount Ida, *Demaree* 47235 (MSC); Norman, *Demaree* 45436 (MSC). POINSETT CO.: Marked Tree, edge of river, *Demaree* 57252 (MSC). POLK CO.: Big Fork, *Moore, s.n.* (MSC). PULASKI CO.: Arkansas River bottom below Natural Steps, *Demaree* 8569 (A, GH, MO, NY). SCOTT CO.: Mill Creek Recreation Area, 5 miles east of Y City, *Donahue* 228 (MSC). SEARCY CO.: Marshall, *Gillis* 3786 (MSC). **Kentucky.** FAYETTE CO.: Lexington, *Hille* 2, (MSC). **Louisiana.** AVOYELLES PARISH: *Bunkie*, *Thieret & Williams* 17663 (MSC). BOSSIER PARISH: Bossier City, *Gillis* 3773 (MSC). CADDO PARISH: Shreveport, *Coty, s.n.* (A). CATAHOULA PARISH: Sicily Island, *Gillis* 5954 (MSC). IBERIA PARISH: Jefferson Island, *Thieret* 17425 (MSC). LAFAYETTE PARISH: Lafayette, *Thieret* 17413 (MSC); MADISON PARISH: Tensas River terrace, Tensas Gun Club Refuge, *Ewan* 17578 (MO). MOREHOUSE PARISH: 4.8 miles north of Oak Ridge, *Gillis* 5946 (MSC). NATCHITOCHES PARISH: small creeks near Clarence, *Demaree* 47360 (MSC). ORLEANS PARISH: New Orleans, *Fendler, s.n.* (MO); New Orleans, *Drummond* 74 (E).PLAQUEMINES PARISH: Pilottown, Delta Wildlife Refuge, *Ewan* 17486 (SMU). RAPIDES PARISH: Alexandria, *Ball* 429 (F, GH, MIN, MO, NY, US). RICHLAND PARISH: north of Girard, *Gillis* 5949 (MSC). ST. LANDRY PARISH: Bayou Carron, near Plaisance, *Thieret & Williams* 17538 (MSC). ST. MARTIN PARISH: St. Martinsville, *Langlois, s.n.* (MIN); Lake Martin, *Thieret* 17402 (MSC). ST. MARY PARISH: Cote Blanche Island, *Thieret* 17443 (MSC). WEBSTER PARISH: locality unknown, *Brown* 5339 (A). WEST FELICIANA PARISH: Catalpa, *Pennell* 4270 (NY). **Mississippi.** ADAMS CO.: 6 miles east of Natchez, *Gillis* 5968 (MSC). LEFLORE CO.: 3.7 miles NE of Itta Bena, *Gillis* 5927 (MSC). QUITMAN CO.: north of Marks, *Gillis* 5919 (MSC). SUNFLOWER CO.: Moorhead, *Gillis* 5932 (MSC); shore of Sunflower River between Moorhead and Indianola, *Gillis* 5935 (MSC). WASHINGTON CO.: east of Leland, *Gillis* 5936 (MSC). **Missouri.** CARTER CO.: Big Spring State Park, *Gillis* 3795 (MSC); west side of Current River north of Big Spring State Park, *Houk & Redfearn* 333 (FSU). HENRY CO.: Windsor Spring, *Hitchcock, s.n.* (MO). IRON CO.: Vulcan, *Smith* 441 (F). JACKSON CO.: Courtney, *Bush* 13892 (A, MIN, MO, ND, NY). ST. LOUIS CO.: Kirkwood, *Woodson* 738 (MIN). **Oklahoma.** LEFLORE CO.: Page, *Palmer* 20948 (A, US). **Tennessee.** RUTHERFORD CO.: Rockvale, limestone glades, *Demaree* 47568 (MSC). SHELBY CO.: Capeville, *Gillis* 5901 (MSC); south of Memphis, *Gillis* 5903 (MSC). **Texas.** ARANSAS CO.: 3 miles NE of Rockport, *Jones* 895 (SMU); Aransas National Wildlife Refuge, *Traverse* 1303 (F, SMU, US). BEXAR CO.: San Antonio, *Jermy, s.n.* (GH, NY). BRAZORIA CO.: Columbia, *Bush* 142 (A, MO, US). BRAZOS CO.: College Station, *Parks* 20714 (SMU); CHEROKEE CO.: Larissa, *Bush* 5589 (A). COLORADO CO.: 5 miles NE of Columbus

on stream bank, *Shinners*, 14612 (SMU). COMAL CO.: New Braunfels, *Lindheimer* 247 (GH, MO, US). COOKE CO.: Gainesville, *Cory* 56120 (SMU). HARDIN CO.: Sour Lake, *Lundell & Lundell, s.n.* (NY). HARRIS CO.: Houston, *Fisher* 33147 (US); North Shore Development, Lake Houston, *Traverse* 1007 (F, US); Bray's Bayou, Houston, *Vines* 242, B-3086, B-3092 (SMU, MSC, US). SAN PATRICIO CO.: Sinton, *Jones* 966 (SMU); Sinton, *Traverse* 1236 (F, SMU, US). WILSON CO.: SE of Floresville, *Parks* 48746 (NY).

The epithet *pubens* is attributed to Engelmann in Watson's Bibliography (1878). It is accompanied by a reference to Gray (1850) who supplied a description in Latin. No type specimen is cited. After Gray's discussion of Lindheimer's collection of *Rhus verrucosa* (see treatment on that topic under *Toxicodendron radicans* subsp. *verrucosum*), he discussed a specimen which he called only "*Rhus toxicodendron var.*". A specimen at the Gray Herbarium fits his description and furthermore was probably seen by Gray. It is labeled "*Rhus toxicodendron* var. *pubens*" in Engelmann's handwriting, probably the source of Watson's attribution of the name to Engelmann. It is the one specimen most likely seen by Watson, the publishing author. Fernald (1941) felt that this specimen was "either the type or isotype." I herewith designate it as the lectotype.

The type comes from the western end of the range of this subspecies where its range overlaps that of subsp. *verrucosum*. The specimen on the lower right of the type sheet has been annotated as *Rhus radicans* var. *verrucosum* (sic) by Fernald, but it is too pubescent for that taxon. It is more likely an intergrade between subsp. *pubens* and subsp. *verrucosum*, bearing the pubescence of the former and the lobing of the latter.

The name *R. toxicodendron* var. *multifolia* Vines is not validly published (no Latin diagnosis), ungrammatically named (should be *multifoliata*), and later abandoned by its author (Vines, 1960). Extra leaflets occur sporadically on individuals in the poison-ivy complex, but are not of population significance, chiefly since plants with extra leaflets generally possess the normal trifoliolate condition as well. The type specimen indicated by the author comes from a park in the city of Houston, Texas, although it was not

marked as the type. It was cited as being in Vine's personal herbarium at the time of the publication of the name, but this herbarium has subsequently been incorporated into the SMU Herbarium.

Subspecies *pubens* is distinguished from subsp. *negundo* by its pilose leaves which are broad, the terminal leaflets often being as wide or wider than long. It occurs in the western Gulf Coastal Plain where subsp. *radicans* is also found. It may be distinguished from subsp. *radicans* by its glabrous fruits and pubescent leaves. Furthermore, the leaflets of subsp. *pubens* usually have coarse teeth on the margins, whereas those of subsp. *radicans* are entire. In Arkansas and Missouri, this subspecies appears to form hybrids over a large area with subsp. *negundo* and to some extent with subsp. *radicans*. At least there is significant diversity over a large area. (See discussion under Hybrids, Crosses, and Intergrades.)

The subspecies is most distinctive in the former Eocene Gulf Embayment, particularly in what is locally called the "delta" region of northwestern Mississippi, southeastern Arkansas, and the eastern part of Louisiana, i.e., the cotton-growing region. From the Mississippi River eastward, the subspecies is replaced abruptly by subsp. *radicans* in the pine region of southern Mississippi. The transition to other taxa is more blurred to the north and west in Tennessee, Arkansas, Missouri, Louisiana, and Texas.

This plant inhabits the southeastern evergreen forest of the Mississippi alluvial plain. Its tree associates are most often *Liquidambar styraciflua*, *Quercus virginiana*, and *Ulmus crassifolia*. Because of the tendency of the plant to be weedy, it often occupies a host of ruderal sites, regardless of the plant associations involved. E. Lucy Braun (1950) describes it as a shrubby component of the oak-hickory forest of the Mississippi embayment section. Its soil preferences are those of terraces of the Old Mississippi Valley south to the present delta. In a few instances it is known from highly calcareous lithosols.

Fig. 40. Type of *Toxicodendron radicans* subsp. *barkleyi* Gillis, *Beaman* 3119.

4e. **Toxicodendron radicans** subsp. **barkleyi** Gillis, subsp. nov. Fig. 40.

Type: *John H. Beaman* 3119. Guatemala, Department of Huehuetenango. Near ruins of Zaculeu on high bank of Rio Zaculeu, 1850 m elevation. Climbing on *Quercus* and other trees; frequent in a local area. Called "Chang" and "Matazanal." 6 August 1959. (MSC-171021, holotype; DUKE, ENCB, GH, NY, TEX, UC, US, isotypes).

Rhus villosum Sessé and Moçiño (as *uillosum*), Pl. Nov. Hisp., p. 47. 1887, non *Rhus villosa* L.f., Suppl. p. 183. 1781, nec Hochet ex A. Rich., Tent. Fl. Abyss. 1: 145. 1847, nec E. Mey. ex Engl. in DC., Monogr. Phaner. 4: 427. 1883, nec Engler, Bot. Jahrb. Supt. 24: 501. 1898. Type: *Sessé and Moçiño, Castillo et Maldonado,* 1787-1795-1804, *No.* 856. "Habitat in Ayahualtempam prope Chilpam et in capite Bonae Spei." (MA, lectotype).

Vitis vel frutex radicellibus aeribus. Folioli integri vel subintegri aut incisuribus interdum, glabrati usque velutini pagina supera folioli, strigosi, pilosi dense, vel tomentosi pagina inferna. Fructi glabri aut puberuli. Differt a subsp. *divaricato* foliis pubescentibus et foliolis aliquantum latioribus, et a subsp. *pubenti* foliolis integribus vel subintegribus et foliolo terminali elliptico seu lanceolato.

Vine or shrub with aerial roots. Leaflets entire or subentire or with occasional notches, ovate to elliptic or elliptic-lanceolate, glabrate to velutinous on the upper leaf surface, strigose, tomentose, or densely pilose on the lower surface. Terminal leaflet blade 3-14 cm long, 1-10 cm broad, petiole 2-12 cm long; terminal petiolule 0.5-5 cm long. Fruits glabrous or puberulent, 3.0-5.0 mm broad. Stem of the season pilose to wooly.

Distribution: Mexico and Guatemala. Fig. 41.

Representative specimens: MEXICO. **Chiapas:** 1 mile north of Jitotol on road to Pueblo Nuevo Solistachuacán, *Breedlove, s.n.* (DS). **Distrito Federal:** Chapultepec Park, Ciudad México, *Bourgeau* 94 (GH); *Gillis* 3726 (MSC). **Durango.** North of Coyotes, Quebrado de San Juan, *Maysilles* 7194 (MICH, US). **Guerrero:** Ayahualtempam near Chilapa, *Sessé and Moçiño* 930 (MA). Omilteme, *Nelson* 7059

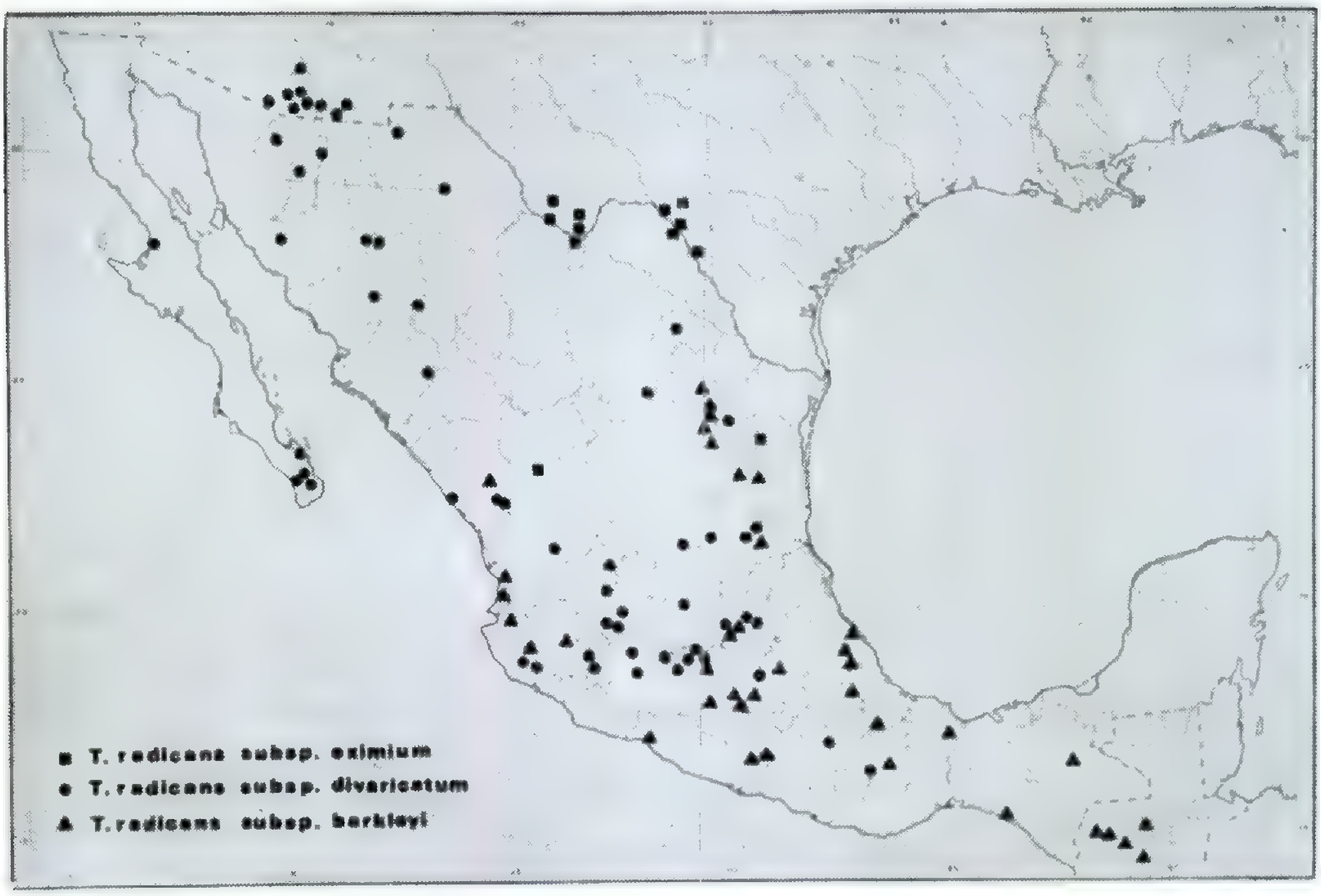

Fig. 41. Distribution of *Toxicodendron radicans* subsp. *barkleyi*, subsp. *divaricatum* and *eximium*.

(US). Vallecitos, Montes de Oca, *Hinton* 10551 (ARIZ, F, GH, NY). Mina, *Hinton* 10492 (A, MO, NY). **Hidalgo:** Rancho Viejo, Municipio de la Misión, *González Quintero* 1002 (MICH, MSC). Tecozantla, *Salazar, s.n.* (US). **Jalisco:** Headwaters of Rio Mascota, 4-7 miles south of El Rincón, road to sawmill called LaCumbre, *McVaugh* 21490 (MICH). Summit of plateau and steep mountainsides above Amacueca, road to Tapalpa, *McVaugh* 20660 (MICH). Summit of pass 7-8 road miles NW of Los Volcanes, between Ayutla and Mascota, *McVaugh* 12195 (MICH). **México:** Tenancingo, *Salazar, s.n.* (TEX). Iztaccihwatl, *Purpus* 269 (MO). **Morelos:** Cuernavaca, *Trelease* 106 (ILL). Tetecala, *Urbino, s.n.* (TEX). Valle del Tepeite, *Lyonnet* 987 (US). **Nayarit:** Oak forest 9 miles north of Compostela, *McVaugh* 18737 (MICH). Arroyo 3.5 miles SW of Jalisco, road to El Malinal, *McVaugh* 14917 (MICH). **Nuevo León:** Alamar about 15 miles SW of Galeana, *Mueller and Mueller* 750 (A, F, TEX). 10 miles south of Monterrey, *Hennen* 67-21 (MSC). Horsetail Fall, SW of El Cercado, 24 miles south of Monterrey, *DeJong* 1818 (MSC, MU). Cerro del Silla, near Monterrey, *Nelson* 6688 (US). **Oaxaca:** San Miquel Alborrados, *Nelson* 534 (US). Cuyamecales, Distrito de Cuicattan, *Conzafta and Gomer, s.n.* (TEX). **San Luis Potosí:** 1.5 miles east of El Plantanito, 20 miles east of Ciudad del Maíz, *McVaugh* 10482 (MICH). **Tamaulipas:** Victoria, *Palmer* 228 (F, GH, MO, NY, US). **Veracruz:** Orizaba, *Botteri, s.n.* (US). Colipa, *Liebman, s.n.* (NY).

Encinal, Matrata, *Matuda* 1368 (A, F). Jalapa, *Smith* 1897 (GH). **Other:** Valle de La Lagima. *Martinez, s.n.* (TEX).

GUATEMALA. **Alta Verapaz:** Coban, *Turchheim* 111784 (GH, NY, US). **El Quiche:** Between San Francisco and Cotzal, *Sharp* 45178 (F). **Guatemala:** San Juan Sacatepequez, *Lewis, s.n.* (F). **Huehuetenango:** Paso de Boquerón along Río Trapichillo below La Libertad, *Steyermark* 51123 (F, TEX). Los Pintos, SW of Huehuetenango, *Steyermark* 48166 (TEX). Near ruins of Zaculeu on bank of Rio Zaculeu, *Beaman* 3119 (DUKE, ENCB, GH, MSC, NY, TEX, UC, US).

This subspecies differs from subsp. *divaricatum* by its pubescent leaves and its somewhat broader leaflets, and from subsp. *pubens* by its entire or subentire leaflets and its elliptic or lanceolate terminal leaflet. The subspecies is named for Dr. Fred A. Barkley, a long-time student of the Anacardiaceae, whose earlier (1937) monographic studies in the poison-ivy complex have been a valuable source of information to this study. Distribution: Mexico: moderate elevations in Sierra Madre Oriental south to Sierra de los Cuchumatanes in Guatemala.

This subspecies is found in the Sierra Madre Oriental, the Sierra Madre del Sur of Mexico, and the Sierra de los Cuchumatanes of western Guatemala. It forms intergrades with subsp. *divaricatum* in the trans-Mexican volcanic belt as far west as southern Jalisco. It is the eastern Mexican counterpart of subsp. *divaricatum*, which occurs in western Mexico although subsp. *barkleyi* was probably not derived from subsp. *divaricatum*, but rather from an ancestral population of subsp. *pubens*. The eastern subspecies has very pubescent leaves, whereas the western one is characterized by glabrous leaves. The leaflet shape and prominence of veins are shared by both subspecies.

The Sessé and Moçiño name *Rhus uillosum* is an enigma. It has been thought to be a misprint for *villosum* because of the frequent interpolation of u's and v's in earlier writing. This suspicion is especially cogent since the leaves are often villous. The name is herein considered to be an orthographic variation of *villosum*.

This subspecies grows chiefly on soils high in calcium, such as the limestones of the Cuchumatanes Mountains and other limestone and calcareous outcroppings of Mexico. It

Fig. 42. *Toxicodendron radicans* subsp. *negundo*. Type of *Toxicodendron negundo* Greene, *Norton* 73.

was found to be abundant on the edge of an orchard in Galeana, Nuevo León, Mexico, where the soil calcium was higher than in any other soil studied: up to 5700 ppm.

4f. **Toxicodendron radicans** subsp. **negundo** (Greene) Gillis, comb. nov. Fig. 42.

Toxicodendron negundo Greene, Leafl. Bot. Observ. Crit. 1: 117. 1905. *Rhus toxicodendron* (subsp.) *negundo* (Greene) Gates, Trans. Kansas Acad. Sci. 41: 106 (nomen nudum), 1938, republished legitimately, Trans. Kansas Acad. Sci. 42: 13. 1939. *Rhus radicans* var. *vulgaris* f. *negundo* (Greene) Fernald, Rhodora 43: 594. 1941. Lectotype: *J. B. Norton* 73. Low woods in Riley County, Kansas. 28 September 1895 (in fruit). US-352742. Isotypes: GH, KSC, MO-1773717, NY, RM-18888. Paratype: *Norton* 73a, same locality, 1896, (in flower). US-352743. Isoparatypes: GH, KSC, MO-1773718, NY, RM-19505.

Toxicodendron aboriginum Greene, Leafl. Bot. Observ. Crit. 1: 125. 1905. Type: *J. M. Bigelow, s.n.*, Indian Territory (Oklahoma), Choctaw Agency, 1853. (US-19845, holotype).

Vine or shrub with aerial roots. Leaflet blade ovate to elliptic, generally notched or serrate, often lustrous in sun forms; glabrate to strigose on the lower surface or with pubescence confined to the veins, not velvety to the touch; no tufts of hairs concentrated in the vein axils below; glabrous on the upper surface with a line of minute curly hairs for several cm along the mid-vein base. Terminal leaflet blade 3.0-20.0 cm long, 1.0-12.0 cm wide, petiole 2.0-16.0 cm long, glabrate, puberulent, hispid, or villous; terminal petiolule 0.5-6.5 cm long. Leaflet tip acute or acuminate; base obtuse or truncate. Fruits glabrous or with a few scattered hairs, 2.5-5.5 mm broad, cream-colored to tan. Branches glabrate to densely puberulent.

Distribution: Canada: southern lobe of Ontario: United States: Great Lakes States south to West Virginia, Kentucky, Tennessee, Arkansas, Oklahoma, west to eastern Kansas, Nebraska, Iowa. Fig. 43.

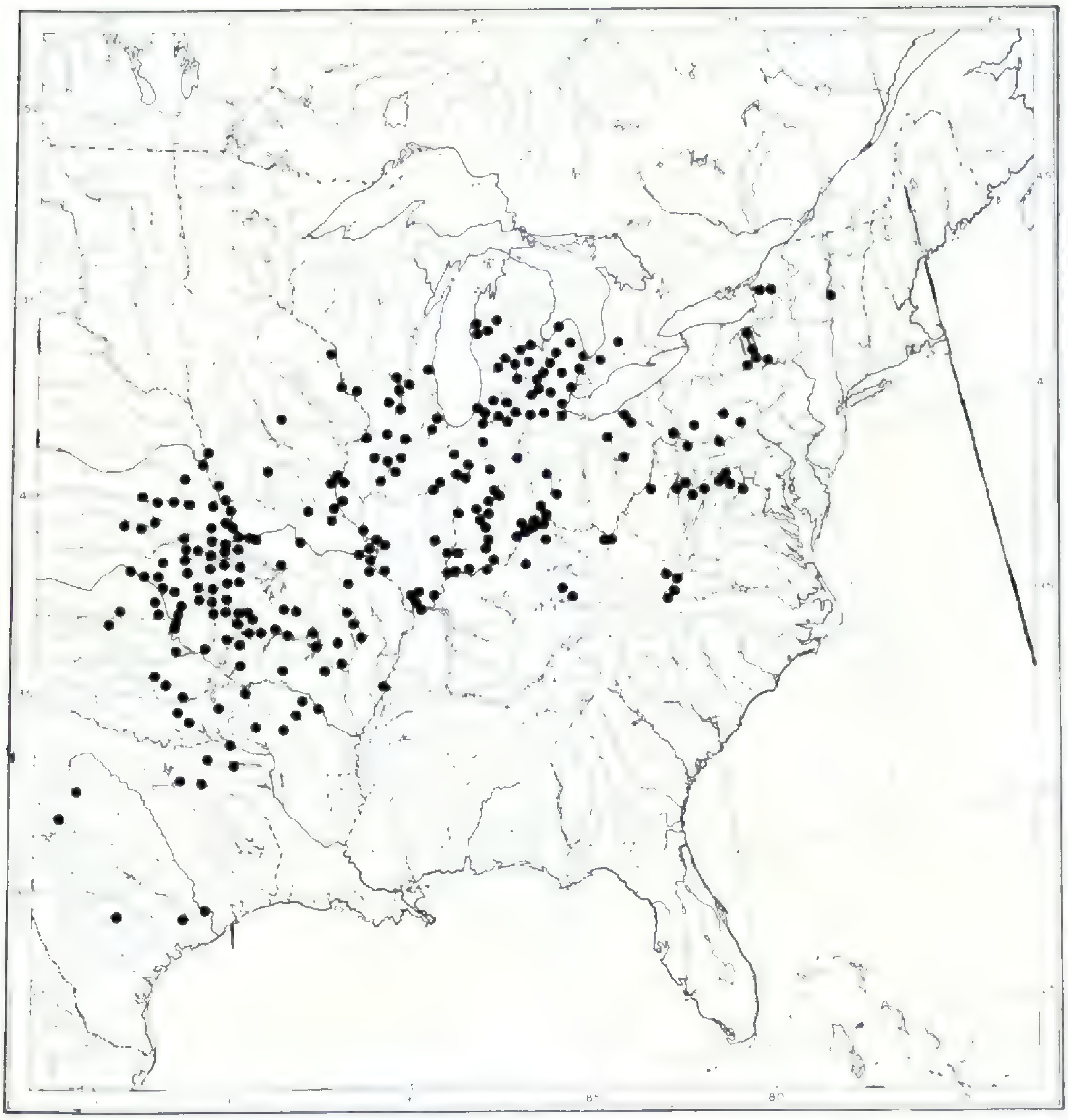

Fig. 43. Distribution of *Toxicondendron radicans* subsp. *negundo.*

Representative specimens: UNITED STATES. **Arkansas:** BAXTER CO.: Norfork, rocky bluffs above Norfork River, *Gillis* 3789 (MSC). BENTON CO.: War Eagle, *Demaree* 6742 (GH, NY, TEX, US). CLARK CO.: Okolona, *Demaree* 17201 (MIN, MO, NY). CLEBURNE CO.: Heber Springs above Greer's Ferry Dam, *Demaree* 45064 (SMU). CRITTENDEN CO.: West Memphis, *Demaree* 11118 (SMU). GARLAND CO.: Hot Springs, *Demaree* 17856 (MO); Magnet Cove, *Palmer* 26617 (A). INDEPENDENCE CO.: Batesville, *Demaree* 17085 (MO, NY). JOHNSON CO.: Knoxville, *Demaree* 19943 (SMU); PERRY CO.: Nimrod, *Demaree* 39638 (MSC). PHILLIPS CO.: Helena, *Palmer* 25097 (A). POLK CO.: base of Rich Mt., *Hopkins & Nelson* 595 (RM); PULASKI CO.: Pulaski Heights, *Demaree* 17319 (MIN); Boyle Park, Little Rock, *Gillis* 3776 (MSC); RANDOLPH CO.: 4 miles SSW Maynard, *Donahue* 216 (MSC). ST. FRAN-

CIS CO.: Forrest City, *Demaree* 47842 (MSC). SEVIER CO.: Bluffs over Little River, Brownstown Ben Lomond, *Demaree* 54004 (MSC). SHARP CO.: Hardy, *Demaree* 27730 (RM, SMU, TEX). **Illinois.** ADAMS CO.: Quincy, *Holton* 174 (F). BUREAU CO.: Ohio, *Ruhl, s.n.* (MO). CALHOUN CO.: Kampsville, *Turner* 467 (F). CHAMPAIGN CO.: Urbana, *Jones* 12640 (MIN, MO, ND, NY). COOK CO.: River Forest, *Eifrig, s.n.* (F); DUPAGE CO.: Naperville, *Powell* 17788 (WIS). HANCOCK CO.: Hancock Twp., *Gates, s.n.* (F). JOHNSON CO.: Tunnel Hill, *Palmer* 15168 (A, MO). KANKAKEE CO.: Kankakee, *Schneider* 671 (F). KNOX CO.: Abingdon, *Batis, s.n.* (A). LAKE CO.: Lake Bluff, *Hutchinson, s.n.* (F). LASALLE CO.: Starved Rock State Park, *Greenman, Lansing, & Dixon* 66 (F, GH, NY); MASON CO.: Bishop, *Chase* 10397 (G). PEORIA CO.: Peoria Heights, *Chase* 9089 (MIN, TEX, WIS). POPE CO.: Golconda, *Palmer* 15390 (A, MO, US). PULASKI CO.: Mounds, *Palmer* 15072 (A, MO, US). RANDOLPH CO.: Red Bud, *Pammel, s.n.* (MO). RICHLAND CO.: Olney, 1818 (F, US); ROCK ISLAND CO.: Park Bryan, *Harper & Harper, s.n.* (A). ST. CLAIR CO.: Cahokia, *Eggert, s.n.* (MO). SANGAMON CO.: Stephenson, Freeport, *Johnson, s.n.* (MIN). TAZEWELL CO.: Kerfoot, *Chase* 10957 (F); VERMILION CO.: between Oakwood and Collison, *Jones* 15599 (MO, WIS); WILLIAMSON CO.: Pittsburg, *Douglass, s.n.* (MO). WOODFORD CO.: south of Spring Bay, *Chase* 12250 (TEX). **Indiana.** CRAWFORD CO.: Milltown, *Deam* 16414 (A); DEARBORN CO.: Aurora, *Deam* 16111 (A). GIBSON CO.: Mt. Carmel, *Tryon* 2805 (F); HARRISON CO.: Elisabeth, *Deam* 16349 (A). HENRY CO.: Mt. Summit, *Kriebel, s.n.* (SMU). HOWARD CO.: Kokomo, *Ek* 57 (US). HUNTINGTON CO.: Huntington College campus, *Henderson, s.n.* (FSU). JEFFERSON CO.: Hanover, *Coulter, s.n.* (F). JOHNSON CO.: Edinburgh, *Deam* 19079 (A). LAGRANGE CO.: Wolcottville, *Deam, s.n.* (SMU). LAWRENCE CO.: Rivervale, *Dean* 17302 (A). MADISON CO.: Ingalls, *Smith* 5619 (F, GH). MONROE CO.: north of Bloomington, *Hawkins, s.n.* (FLAS). NEWTON CO.: Kankakee River State Park, *Thieret* 1295 (F). ORANGE CO.: West Baden, *Deam* 17336 (A). OWEN CO.: McCormack Creek, *Deam* 17519 (A). PERRY CO.: Cannelton, *Deam* 16618 (A). POSEY CO.: Shelton, *Heiser, s.n.* (MSC). PUTNAM CO.: Green Castle, *Grimes* 531 (US). RIPLEY CO.: Laugherty Creek, east of Versailles, *Deam* 16132 (A); ST. JOSEPH CO.: South Bend, *Nieuwland, s.n.* (MO). SWITZERLAND CO.: Cross Plains, *Deam* 16183 (A). TIPPECANOE CO.: West Point, *Gillis* 4274 (MSC). VANDERBURG CO.: Evansville, *Deam* 16781 (A). VERMILLION CO.: Blanford, *Freisner* 19505 (NY). WARRICK CO.: Yankeetown, *Deam* 16711 (A). WELLS CO.: Harrison Twp., *Deam, s.n.* (GH, MIN, MO, US, WIS). WHITE CO.: Furnessville, *Johnson, s.n.* (NY). **Iowa.** CLAYTON CO.: McGregor, *Shimek, s.n.* (WIS). DECATUR CO.: without definite locality, *Anderson, s.n.* (MIN, MO, RM). FAYETTE CO.: Fayette, *Fink, s.n.* (MIN). JOHNSON CO.: Iowa City, *Hitchcock, s.n.* (MIN.). LEE CO.: Keokuk, Jackson Twp., *Hayden* 9364 (GH, MIN, MO, NY). STORY CO.: Ames, *Hitchcock, s.n.* (MO). **Kansas.** ALLEN CO.: without

definite locality, *Hitchcock, s.n.* (KSC). ANDERSON CO.: without definite locality, *Hitchcock, s.n.* (KSC). BARBER CO.: Hardtner, *McGregor* 14822 (SMU). BARTON CO.: without definite locality, *Hitchcock, s.n.* (KSC). BROWN CO.: without definite locality, *Clothier & Whitford, s.n.* (KSC). BUTLER CO.: White Water, *Hitchcock, s.n.* (KSC). CHASE CO.: without definite locality, *Hitchcock, s.n.* (KSC). CHEROKEE CO.: Elm Branch, *Jacobs, s.n.* (KSC); COFFEY CO.: LeRoy, *Dunfield, s.n.* (KSC). CONCORDIA CO.: without definite locality, *Hitchcock, s.n.* (KSC). COWLEY CO.: Arkansas City, *Palmer* 22101 (A, US). CRAWFORD CO.: without definite locality, *Clothier & Whitford, s.n.* (KSC). DOUGLAS CO.: Lawrence, *Gillis* 6484A (MSC). ELK CO.: without definite locality, *Clothier & Whitford, s.n.* (KSC). ELLSWORTH CO.: Terra Cotta, *McGregor* 12644 (US); FRANKLIN CO.: without definite locality, *Hitchcock, s.n.* (KSC). GEARY CO.: Alida, *Gates* (KSC). JACKSON CO.: without definite locality, *Clothier & Whitford, s.n.* (KSC). JEFFERSON CO.: Perry, *Clothier, s.n.* (KSC). JOHNSON CO.: without definite locality, *Pinchomb, s.n.* (KSC). KIOWA CO.: without definite locality, *Hitchcock, s.n.* (KSC). LABETTE CO.: Montana, *Rydberg & Imler* 305 (KSC, NY). LINCOLN CO.: without definite locality, *Hitchcock, s.n.* (KSC). LINN CO.: Pleasanton, *Hitchcock, s.n.* (KSC). MARION CO.: without definite locality, *Hitchcock, s.n.* (KSC). MITCHELL CO.: Beloit, *Hitchcock, s.n.* (KSC). MONTMORENCY CO.: without definite locality, *Hitchcock, s.n.* (KSC). MORRIS CO.: Kelso, *Good* 29 (KSC). NEMAHA CO.: Aenida, *Hitchcock, s.n.* (KSC). NEOSHO CO.: without definite locality, *Hitchcock, s.n.* (KSC). OSAGE CO.: Burlingame, *Hitchcock, s.n.* (KSC). OSBORN CO.: Downs, bank of Solomon River, *Palmer* 21335 (A). OTTAWA CO.: without definite locality, *Hitchcock, s.n.* (KSC). POTTAWATOMI CO.: Floersh, *Haymaker, s.n.* (KSC); Onaga, *Day, s.n.* (KSC). REPUBLIC CO.: T. 4S., R. 3W., SW 1/4 Sec. 27, *Morley* 308 (SMU). RICE CO.: without definite locality, *Hitchcock, s.n.* (KSC). RILEY CO.: without definite locality, *Norton* 73, 73a, (GH, KSC, MO, NY, RM, US); ROOKS CO.: Rockport, *Bartholemew, s.n.* (MO). SALINE CO.: Gypsum City, *Palmer* 21329 (A, US). SEDGWICK CO.: without definite locality, *Clothier & Whitford, s.n.* (KSC). SHAWNEE CO.: Topeka, *Popenoe, s.n.* (KSC). SMITH CO.: without definite locality, *Hitchcock, s.n.* (KSC). SUMNER CO.: Belle Plaine, *Gates* 19279 (KSC). Wabaunsee, *Gates* 21617 (KSC). WASHINGTON CO.: Linn, *Dodd, s.n.* (KSC). WILSON CO.: Neodesha, *Palmer* 21152 (A); Roper, *Haller, s.n.* (KSC). WYANDOTTE CO.: without definite locality, *Clothier & Whitford, s.n.* (KSC). WOODSON CO.: without definite locality, *Lathrop* 391 (US). **Kentucky.** BALLARD CO.: without definite locality, *Anderson, s.n.* (GH, MO). BOYD CO.: Catlettsburg, *McCoy, s.n.* (GH). CHRISTIAN CO.: Pennyrile Forest State Park, *Donahue* 210 (MSC). FAYETTE CO.: 8 miles north of Kentucky River, *Gillis* 6534 (MSC). JEFFERSON CO.: Louisville, N.G.R.R., *Mueller* 447 (HY). KENTON CO.: 2 miles south of Erlanger, *Gillis* 6315 (MSC). LAUREL CO.: 0.6 mile north of high-

way 30, *Gillis* 6538 (MSC). NELSON CO.: 4 miles south of Bardstown, *Donahue* 274 (MSC). ROCKCASTLE CO.: 0.6 mile north of Roundstone Creek, 7.9 miles north of Mt. Cernon, *Gillis* 6535 (MSC). SCOTT CO.: 1.5 miles north of Georgetown, *Gillis* 6532 (MSC). **Maryland.** MONTGOMERY CO.: Plummer's Island in Potomac River, *Kearney, s.n.* (US). **Michigan.** ARENAC CO.: AuGres Twp., *Gillis* 3599 (MSC). BARRY CO.: Maple Grove Twp., *Gillis* 3575 (MSC); Wall Lake, *Gillis* 3595 (MSC). BERRIEN CO.: Three Oaks Twp., Warren Woods, *Gillis* 3510 (MSC); Grand Beach, *Nieuwland, s.n.* (ND, MSC). BRANCH CO.: Coldwater, *Gillis & Wetmore* 2871 (MSC). CALHOUN CO.: Athens, *Gillis* 3503 (MSC); Bedford Twp., *Gillis* 2804 (MSC). CASS CO.: Vandalia Twp., *Gillis* 3509 (MSC); CLARE CO.: Clare, *Flicke, s.n.* (MSC). CLINTON CO.: Rose Lake Bog, *Howell & Roberts, s.n.* (MSC); EATON CO.: Thornapple River bank, *Gillis* 4273 (MSC). GENESSEE CO.: Montrose, *Gillis* 3483 (MSC). GRATIOT CO.: Bethany Twp., *Gillis* 5487 (MSC). HILLSDALE CO.: intersection of Custer and Grace Roads, *Gillis* 4141 (MSC). HURON CO.: Charity Island, Saginaw Bay, *Dodge, s.n.* (GH). INGHAM CO.: Haslett, *Gillis* 2850 (MSC); East Lansing, bank of Red Cedar River, *Gillis* 2517 (MSC). IONIA CO.: Morrison Lake, *Muma, s.n.* (MSC). ISABELLA CO.: Mt. Pleasant, *Gillis* 3075 (MSC). JACKSON CO.: *Jackson* 2558 (MSC). KALAMAZOO CO.: adjacent to Gull Creek, *Fischer, s.n.* (MSC). KENT CO.: Cascade Twp., along Thornapple River, *Hoffman, Swan, & Sarkissian* 338 (MSC); LENAWEE CO.: Seneca Twp., *Gillis* 3548 (MSC); LIVINGSTON CO.: SW of Pinckney, *Hiltunen* 2096 (WUD); Hamburg, *Farwell* 8343 (BLH). MACOMB CO.: Washington, *Cooley, s.n.* (MSC). MASON CO.: Scottville, *Gillis* 3546 (MSC). MECOSTA CO.: Colfax Twp., *Gillis* 3591 (MSC). MIDLAND CO.: Midland, *Erbisch* 1 (MSC). MONROE CO.: Clark Island, *McDonald, s.n.* (MSC). MONTCALM CO.: Stanton, *Gillis* 3574 (MSC). MUSKEGON CO.: North Muskegon, *Gillis* 5427. NEWAYGO CO.: Ashland Twp., *Gillis* 3583 (MSC). OAKLAND CO.: Proud Lake Recreation Area, *Gillis* 2586 (MSC); Farmington, *Mühling, s.n.* (MSC). OGEMAW CO.: West Branch, *Gillis* 3533 (MSC). OSCEOLA CO.: Sylvan Twp., *Gillis* 3480 (MSC). ST. CLAIR CO.: Port Huron, *Dodge* 3784 (SMU, BLH, NY, TEX, E). ST. JOSEPH CO.: Mendon, *Gillis* 3506 (MSC). SHIAWASSEE CO.: Woodhill Twp., *Gillis* 3479 (MSC). TUSCOLA CO.: Vassar, *Gillis* 5000 (MSC). VAN BUREN CO.: Bangor Twp., *Gillis* 3521 (MSC). WASHTENAW CO.: Ann Arbor, *Sudworth, s.n.* (US). WAYNE CO.: Belle Isle, *Farwell* 1492 (BLH). **Minnesota.** HOUSTON CO.: Houston Village, *Butters & Rosendahl* 3014 (GH). **Missouri.** ADAIR CO.: Novinger, *Palmer* 25504 (A, MO). ATCHISON CO.: Watson, *Palmer* 18912 (A, MO, US). BARRY CO.: Roaring River State Park, *Donahue* 222 (MSC). BENTON CO.: Cole Camp, *Palmer* 30035 (A, MO). CARTER CO.: Big Spring State Park, *Donahue* 220 (MSC); CLARK CO.: Dumas, *Palmer* 21882 (A). GREENE CO.: Springfield, *Standley* 8627 (US). HENRY CO.: Windsor, *Hitchcock, s.n.* (MO). HOLT CO.: Forest City, *Palmer* 25402 (A, MO). JACKSON

CO.: Kansas City, *Bush* 10103 (MO). JASPER CO.: LaRussel, *Palmer* 1517 (MO). JACKSON CO.: Independence, *Bush* 9365 (A, F, MO). JEFFERSON CO.: Kemmswick, *Wislizenus, s.n.* (MO). JOHNSON CO.: Columbus, *Palmer* 36615 (A, MO). MARION CO.: Hannibal, *Davis, s.n.* (A, MO). MCDONALD CO.: Noel, *Bush* 5757 (A, US). OZARK CO.: Pontiac, *Palmer* 34792 (A, MO). PHELPS CO.: Jerome, *Kellogg* 310 (MINN, MO). RALLS CO.: Bear Creek, *David, s.n.* (MO). ST. LOUIS (city); *Emig* 287 (MO). ST. LOUIS CO.: Allenton, *Letterman, s.n.* (MIN, MO, NY, US). SHANNON CO.: Montier, *Bush* 144 (M). STONE CO.: Galena, *Palmer* 23879 (A). TANEY CO.: Branson, *Palmer* 4714 (A, E, MO). WEBSTER CO.: Seymour, *Donahue* 221 (MSC). **Nebraska.** CHERRY CO.: Lancaster, wooded banks of Salt Creek, *Turrell, s.n.* (ARIZ). SARPY CO.: Bellevue, *Eastman, s.n.* (NY). WEBSTER CO.: Red Cloud, *Bates, s.n.* (MIN). **New York.** BROOME CO.: Mount Glenwood Ravine, Binghamton, *Millspaugh, s.n.* (F). CAYUGA CO.: Montezuma, *Eames, Wiegand, & Randolph* 12399 (GH). CHEMUNG CO.: East Elmira, *Johnson, s.n.* (NY). FRANKLIN CO.: Brushton, *Cutler, s.n.* (MSC). JEFFERSON CO.: Plessis, *Gillis* 5376 (MSC); MURRAY CO.: Price's Falls, *Demaree* 12891 (MIN). SENECA CO.: Magee, *Gillis* 3804 (MSC). TIOGA CO.: without definite locality, *Millspaugh, s.n.* (US). TOMPKINS CO.: Ithaca, Cascadilla Creek, *Palmer* 768 (GH). **Ohio.** BUTLER CO.: Oxford, *Overholts, s.n.* (MO). COSHOCTON CO.: Coshocton, *Moldenke* 12788 (SMU). GREENE CO.: Yellow Springs, *Demaree* 11455 (A, GH, MIN, MO, NY, SMU, WIS). HAMILTON CO.: Cincinnati, *Lloyd, s.n.* (MIN). LUCAS CO.: Sylvania, *Wilson* 1512 (WIS). SANDUSKY CO.: Cedar Point, *Jennings & Jennings, s.n.* (ND-G). SHELBY CO.: 2.9 miles north of McCartyville, *Gillis* 5431 (MSC). SUMMIT CO.: Cuyahoga River, Akron, *Folz, s.n.* (MIN, US). **Oklahoma.** ADAIR CO.: Watts, *Wallis* 8171 (SMU). CADDO CO.: False Washita River between Fort Cobb and Fort Arbuckle, *Palmer* 58 (NY, US). CANADIAN CO.: Yukon, *Palmer* 22120 (A). CHEROKEE CO.: limestone escarpments 8 miles north of Talequah, *Hopkins* 3127 (TEX). CLEVELAND CO.: Norman, *Goodman, s.n.* (MSC). COMMANCHE CO.: West Cache Creek, Wichita Mts., *Nagle, s.n.* (US). CREEK CO.: Sapulpa, *Bush* 57 (MO). DELAWARE CO.: Dripping Springs, *Wallis* 8180 (SMU). JOHNSTON CO.: Tishomingo, *Palmer* 6412 (A, MO, US). KAY CO.: without definite locality, *White, s.n.* (NY). LEFLORE CO.: Choctaw Agency (Skullyville), *Bigelow, s.n.* (US). MCCURTAIN CO.: Boss, *Houghton* 3718 (GH, MO, NY). MURRAY CO.: Platt National Park, *Merrill & Hagen* 1124 (F). OTTAWA CO.: Commerce, *Bush* 10142 (A, GH, MO, NY). PAYNE CO.: 2 miles west of Stillwater, *Cockrell* 43 (TEX). PONTOTOC CO.: Ada, *Robbins* 2500 (SMU). PUSHMATAKA CO.: Clayton, *Waugh* 124 (MO). SEQUOYAH CO.: Gore, *Wallis* 8430 (SMU). Woods CO.: without definite locality, *White, s.n.* (MIN, RM). **Pennsylvania.** ALLEGHENY CO.: Mt. Lebanon Twp., along creek in Kennedy's wood, *Churchill, s.n.* (MSC). DAUPHIN CO., Harrisburg, *Small, s.n.* (F, US). FULTON CO.: between Tuscarora and Sideling Mountains, *Gillis* 5113

(MSC); Knobsville, *Gillis* 5116 (MSC). INDIANA CO.: Homer City, *Wahl* 1725 (SMU). MIFFLIN CO.: Reedsville, *Fogg* 16790 (NY). **South Dakota.** CLAY CO.: river bottom, *Taxonomy Class of 1955* (SDU). **Tennessee.** DAVIDSON CO.: Nashville, near confluence of Mill Creek and River, *Bartlett* 3381 (MICH, MSC). **Texas.** BEXAR CO.: without definite locality, *Parks*, B-50, B-66 (MO, MSC). COOKE CO.: Gainesville, *Shinners* 13236 (SMU). DALLAS CO.: Dallas, *Reverchon, s.n.* (GH). FORT BEND CO.: Richmond, *Bray* 80 (US). HARRIS CO.: Houston, *Eggert, s.n.* (MO); San Jacinto, *Boon* 20002 (MO). HUNT CO.: Commerce, *Shinners* 12265 (SMU). JACKSON CO.: Ganado, *Palmer* 9233 (A, MO). KARNES CO.: Panna Maria, *Johnson* 1300 (SMU). KAUFMAN CO.: Terrell, *Tyler, s.n.* (US). RED RIVER CO.: Clarksville, *Cory* 56041 (US). TAYLOR CO.: Abilene, *Talstead* 7657 (GH). TOM GREEN CO.: San Angelo, *Palmer* 11137 (A, MO). WOOD CO.: Hawkins, *Gillis* 3769 (MSC). **Virginia.** FREDERICK CO.: Chambersville, *Gillis* 5705 (MSC). GILES CO.: Pembroke, *Fogg* 14773 (GH, MIN, MO). LOUDOUN CO.: 1 mile down Limestone Branch from highway 15, *Allard* 21392 (US). MONTGOMERY CO.: Blacksburg, *Adams & Wherry* 2230 (A, GH, US). WESTMORELAND CO.: Colonial Beach, *Tidestrom & Bartlett* 5938 (US). **West Virginia.** CABELL CO.: Milton, *Williams* 379 (GH); Huntington, *Gilbert* 186 (GH). GRANT CO.: Mt. Storm, east flank, *Gillis* 5720 (MSC). JEFFERSON CO.: Charles Town, Byrd roadside park, *Gillis* 5701 (MSC); Harper's Ferry, *Gillis* 5700 (MSC). MINERAL CO.: Burlington along Patterson Creek, *Gillis* 5714 (MSC). PRESTON CO.: Erwin on Wolf Creek, *Gillis* 5721 (MSC). RITCHIE CO.: Berea, *Randolph & Randolph* 1385 (GH). TUCKER CO.: Blackwater River, *Moore* 2115 (GH). UPSHUR CO.: Buckskin, *Pollock, s.n.* (KSC). **Wisconsin.** DANE CO.: Mazomanie, *Seymour* 11500 (WIS). GRANT CO.: Rockville, *Wunderlin, s.n.* (WIS). MASON CO.: Bath, *Guther* 7517 (WIS). MILWAUKEE CO.: without definite locality, *Russell, s.n.* (GH). RACINE CO.: Racine, *Hale, s.n.* (WIS). ROCK CO.: Avon, *Fassett* 28113 (WIS). SAUK CO.: *Smith* 53928 (MIL).

CANADA. **Ontario.** CARLETON CO.: March Twp., *Dore & Breitung* 8516 (E). GRENVILLE CO.: Prescott, *Dore* 18622 (MSC). MIDDLESEX CO.: Poplar Hill, *Gillis* 5370 (MSC). NORFOLK CO.: *Williams, s.n.* (A), *Richardson, s.n.* (A). WATERLOO CO.: Galt, *Montgomery* 893 (GH). Baden, *Gillis* 5581 (MSC).

Gates published the trinomial *Rhus toxicodendron negundo* in a species list in 1938, followed it a year later with a formal descrption. He did not clearly designate a rank for the epithet *negundo*, but included this enigmatic statement: "The trinomial in botany is usually referred to as a variety, although the designation subspecies would appear to be more reasonable." Even though no rank is clearly stated, it would appear that Gates intended the rank

of subspecies. His 1939 publication should be considered the legitimate and valid publication because it refers to a previously and effectively published name (*Toxicodendron negundo* Greene). Greene described the fruits of his taxon, *Toxicodendron negundo*, as "uncommonly small . . . the length distinctly greater than the thickness," neither character being borne out by the type material.

The type for *Toxicodendron aboriginum* was collected at Choctaw Agency, Indian Territory by J. M. Bigelow on the Whipple Expedition. Although there is no Choctaw Agency today, Gaspare Signorelli (personal communication), philatelic history specialist, informs me that this locality was a small settlement now known as Skullyville, Oklahoma. It was "Choctaw Agency West," just across the border from Arkansas Territory in what is now northern LeFlore County. Greene's description "abruptly apiculate" for the leaflets does not fit the type material which has acuminate leaflets. The fruits have a scattered pubescence which will be discussed later.

It seems strange that this common plant of the mid-western United States should have no formal subspecies or variety name until now. Most manual writers presume that the typical variety is this one and that the Atlantic Coast subspecies must be one which was described later, rather than the other way around. Such presumptions, of course, fly in the face of the historical evidence that the earliest collections in America were from the Coastal regions, and not the interior.

It has been difficult to characterize this subspecies, largely because of the distinctive characters it does *not* have. It does not have the lobed margins of subsp. *eximium* nor of subsp. *verrucosum*, nor the consistently entire or subentire margins of subspp. *radicans, orientale, hispidum, barkleyi,* nor *divaricatum,* nor the pubescent fruits of subspp. *radicans, eximium,* etc. Rather, it possesses a variable and moderate degree of pubescence on the leaflets, occasionally scattered-pubescent fruits, some notching on the leaflets, which are clusters of characters found to some degree in other subspecies.

Miller (Gard. Dict. Art. *Toxicodendron*, No. 6, 1768) may have had reference to this taxon in his *Toxicodendron volubilis* (sic). The description of "trifoliate leaves whose lobes are oval, smooth, and cut into sinuses" does not wholly apply, and could relate to other taxa, but also might fit this one. Miller's reference to Dillenius's *Hort. Elth.* seems to provide a lead, but it is to *Toxicodendron amplexicaule, foliis minoribus glabris*, which cannot be typified. There is sufficient doubt as to whether Miller's plant refers to subsp. *radicans* or to subsp. *negundo* that the basionym *volubile* cannot be used. In all likelihood, evidence suggests that, since most specimens available to eighteenth century England were coastal forms, Miller had probably never seen this subspecies.

This subspecies intergrades with *Toxicodendron rydbergii* at its western and northern limits and along Lake Michigan. It intergrades with subsp. *radicans* in the Appalachians, especially the Allegheny ridge and the Blue Ridge Mountains. It seems to form large populations of intergrades with subsp. *pubens* in Arkansas and southern Missouri where the infraspecific boundaries become obscured.

Although subsp. *negundo* and subsp. *radicans* have been confused because of their similarity, the closest relationship of subsp. *negundo* seems to be with subsp. *pubens*. These two subspecies are sympatric in Arkansas and Missouri. Subspecies *pubens* is possibly a specialized, pubescent form from more generalized *negundo* stock. The differences are mainly quantitative ones in degree of pubescence, length-to-width ratio of leaflets, and degree of notching or serration of leaflets.

Some populations of subsp. *negundo* possess a slightly pubescent fruit, reminiscent of the fruits of subsp. *radicans*, under which name Barkley (1937) included them. These populations appear in a few places in northwestern Indiana, the Ohio River counties of Indiana (Deam, 1940), and a few places in eastern Oklahoma. In no way, other than the slightly pubescent fruits, do these plants seem to diverge from the more typical subsp. *negundo*, and they do not

possess the entire leaflets, nor tufts of hairs on the lower leaflet surface characteristic of subsp. *radicans*.

Toxicodendron radicans subsp. *negundo* is frequent in beech-maple, elm-ash, elm-maple, and weedy plant associations. In southeastern Wisconsin, at the northwestern extent of its range, it has been described from the mesic and lowland southern forests (Curtis, 1959). Farther to the south it is a constant species in the northern Appalachian highland division of the hemlock-white pine-northern hardwoods of the Alleghenies and the mixed mesophytic forest and western mesophytic forest of the central states (Braun, 1950), but it is not found in similar forests in the northern reaches of the country such as upper Michigan, Wisconsin, New York, and New England. There it is replaced by the less abundant *T. rydbergii*.

Whereas its related taxon, subsp. *pubens*, is a component of the oak-hickory woods, this subspecies and its other relative, subsp. *radicans*, are seldom found in the dry, undisturbed oak-hickory forest of the northeastern or central United States. Although it is difficult to prove negative associations, more than 58 oak-hickory stands have been examined in the northeastern United States in only four of which poison-ivy has been found. It was usually in a marginal state of existence as a chance invader. Its existence is also marginal in scrub-oak and pine woods of the Coastal Plain or the jack-pine plains of Michigan. It is generally replaced on open dunes by *Toxicodendron rydbergii*, but may appear in the dune forests. Other than these habitat preferences, it occupies habitats similar to those in which subsp. *radicans* occurs.

(To be continued)

OBSERVATIONS ON MICROCOLEUS LYNGBYACEUS (KÜTZ.) CROUAN FROM MARINE HABITATS IN NEW ENGLAND[1]

E. E. WEBBER[2]

Speciation in the Cyanophyta traditionally has emphasized morphological characteristics. Such features as cell size, the absence or presence and nature of a sheath, patterns of branching, presence and arrangement of heterocysts and akinetes, etc., are all familiar criteria used to discern the various families, genera, and species of bluegreen algae.

Within recent years, increasingly critical examinations of both field and cultured material have revealed a high incidence of morphological plasticity among numerous cyanophytes, such plasticity being hitherto either unknown or unappreciated.

Treating only the coccoid Cyanophyceae, Drouet & Daily (1956) showed that many genera and species are ecological variants of a smaller number of entities. For example, 78 taxa were shown by these authors to be ecophenes of one species, *Entophysalis deusta*. In culture studies with this organism, van Reine & van den Hoek (1966) more recently have induced morphological variants previously recognized as 4 genera.

While still comparatively few in number, some studies have been made on the filamentous bluegreen algae. The most ambitious efforts directed toward a more accurate interpretation of variation among filamentous forms have been those of Drouet (1962, with *Microcoleus vaginatus;* 1963, with *Schizothrix calcicola;* 1964, with *Microcoleus chthonoplastes;* 1968, with the Oscillatoriaceae). In addi-

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[2]The author appreciates the constructive criticisms of Dr. Francis Drouet and Dr. John Blum in the preparation of this manuscript.

tion, studies of filamentous bluegreens which further support the inappropriateness of the older taxonomic criteria are those of Stein (1963) and Pearson & Kingsbury (1966).

The occurrence of ecophenes among Massachusetts salt marsh populations of filamentous cyanophytes (Webber, 1967) has prompted further study of these interesting plants. A continuing field and laboratory research program of New England coastal bluegreen algae by this author is in progress.[3]

The present paper describes the ecophenes of *Microcoleus lyngbyaceus* as they occur at several New England coastal stations. The ecophenes of *Microcoleus lyngbyaceus* (Kütz.) Crouan reported here are *Hydrocoleum lyngbyaceum* Kütz., *H. glutinosum* (Ag.) Gom., *H. holdenii* Tilden, *Lyngbya aestuarii* (Mert.) Lieb., *L. confervoides* C. Ag., and *L. semiplana* (C. Ag.) J. Ag. Field and laboratory data gathered by the present author from 1967 to 1970 illustrate the morphological plasticity of this common filamentous alga. This evidence, along with that of Drouet (1968), shows that the "species" of *Hydrocoleum* and *Lyngbya* listed above are actually growth forms of a single entity, *Microcoleus lyngbyaceus,* and should not be recognized as discrete taxa.

Collecting stations for the above data include Cape Neddick, Maine (salt marsh), Adams Point, New Hampshire (salt marsh), and Ipswich, Salem, and Nahant, Massachusetts (salt marshes and rocky coast). All specimens have been deposited in the author's herbarium.

Most results reported here were obtained from immediate study of field collected plants. Some data, however, came from cultures. Culture innoculations were made by snipping pieces of trichomes from field collected material and growing them in Erd-Schreiber medium (Provasoli, et. al., 1957) at 12° C under a 12-hour light/dark regime, unless otherwise indicated.

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[3]Supported by grants from Sigma Xi and the American Philosophical Society.

Discussion of Collections

CAPE NEDDICK, MAINE: *Microcoleus lyngbyaceus* occurs commonly as the *Lyngbya aestuarii* form mixed with *Vaucheria compacta* in the mud of the lower littoral zone. Plants were collected in September, 1967 and were grown in culture for two months. During this period, trichomes of a variety of colors, bluegreen, green, and brown, became apparent; in addition, some trichomes had terminal cells with inflated outer walls, while others lacked this feature. All trichomes were of the same width, regardless of color and the nature of the terminal cell; both characteristics were used previously in *Lyngbya* species determinations.

ADAMS POINT, NEW HAMPSHIRE: The abundance of *M. lyngbyaceus* was apparent here as macroscopic, black, curly growths in the mud of the Spartinetum alternifloretum. Microscopically, the trichomes were variable in size and in pigmentation. Some measured 13-17 μ wide and were bright bluegreen (*Hydrocoleum lyngbyaceum* and *H. glutinosum*). Others ranged in width from 25-35 μ, and were yellow-brown with broadly rounded terminal cells (*H. holdenii*). Very common, however, were plants 30 μ in width and grading in pigmentation from bluegreen to yellow; equally common were numerous trichomes 35 μ wide and bluegreen in color. Further, trichomes ranging in width from 17-35 μ and encompassing all color gradations from bluegreen to yellow-brown occurred within the same common sheath (coll. 30-69).

IPSWICH and SALEM, MASSACHUSETTS: Preliminary indications of the weakness of criteria used to delineate *Hydrocoleum lyngbyaceum, H. glutinosum,* and *H. holdenii* at an Ipswich salt marsh have been reported (Webber, 1967). Additional collections at this salt marsh made in June, 1968 from mud banks of Fox Creek and from the mud substratum of *Salicornia europaea* on the marsh surface yielded plants whose dimensions and colorations further negate the discreteness of the above mentioned "species".

From these collections I have observed trichomes to move out of the common sheath, i.e., the *Hydrocoleum* form, in which case, after assuming a thick and individual sheath, they then resembled the several species of *Lyngbya* cited above (coll. 12, 13, 15, 16).

Additional collections of *M. lyngbyaceus* have been made (summer, 1970) from an estuarine habitat in Salem, Massachusetts. The plants occur as black films on salt marsh soil at the mouth of this estuary (Salem Harbor), where they have a macroscopic appearance similar to that described above for their presence at Adams Point, N.H. At the head of the marsh approximately ½ mile upstream (Forest River) the alga is apparent as green-black "skins" floating at the surface of the water. At both extremes of this estuarine system, *M. lyngbyaceus* occurs as the *Hydrocoleum holdenii* form. Cultures of this entity were maintained at room temperature for two weeks. At the end of this growth period, the plants exhibited very little organization of the *Hydrocoleum* type. Rather, many trichomes became freed from their common sheath and, as was noted with the Ipswich plants, assumed a *Lyngbya* morphology. In addition, these trichomes showed considerable overlap in those features used traditionally as species criteria, i.e., cell diameters, morphological details of the terminal cell, and pigmentation. Thus, "species determinations" of *Lyngbya confervoides, L. aestuarii, Hydrocoleum glutinosum,* and *H. holdenii* were possible from this cultured material.

NAHANT, MASSACHUSETTS: The habitats of *Microcoleus lyngbyaceus* at Nahant consist of variously sized tide pools and moist rock crevices. Daily summer water temperature and salinity fluctuations in these pools may be either slight or great depending upon their vertical shoreline location, their size, and their degree of exposure to sunlight and wave action. For example, temperature differences between incoming tidal waters and those of the pools may vary from only a few degrees to as much as 11° C. On hot summer days with incoming tides temperature fluctua-

tions of 3-4° C occur several times each minute in the mid to upper littoral pools. On the other hand, and under the same tidal conditions, pools approximately one foot higher upshore undergo increasingly marked temperature changes of a 12° C magnitude, these changes occurring regularly at approximately 3 minute intervals. By far the greatest temperature extremes are to be found in the highest level rock pools, such temperatures commonly exceeding that of the sea water by 18-21° C. The instantaneous vaporization of the sea water as it splashes against the intertidal rocks is clearly indicative of the higher temperatures typical of this segment of the shore.

Salinities in these high rock pools were the maximum recorded along the shore. While these measurements could not be determined precisely, due to the limits of the salinometer used, they were strongly in excess of 42 ‰.

Microcoleus lyngbyaceus is common along these rocky shores in small (1-8″ deep) upper littoral tide pools, the plant mass appearing macroscopically as skeins of blue-black, orange, or orange-brown material typically 2-3 cm long; microscopically, these are the *Lyngbya* forms (e.g., coll. 11-69). In the deeper (20″) pools, however, filaments of this species were entwined in such a way that they became structured into 6-8″ long gas-filled, brown tubes standing erect from the pool bottom (coll. 32-69). Individual trichomes of these tubes measured 26 μ wide; filament diameters were commonly 52 μ, the non-lamellated sheaths having roughened margins. The terminal cells of these filaments often had clear and inflated outer walls; hormogonia were abundant. Some of the trichomes comprising these hollow tubes were contained within an obvious common sheath (the *Hydrocoleum* form), while others were not so contained (the *Lyngbya* form).

Additional plants of the *Lyngbya* type from the smaller pools, when cultured at room temperatures for three weeks, changed their morphology and assumed that of *Hydrocoleum*, i.e., several trichomes in twisted strands enveloped by a common sheath (coll. 15-69). Further, plants of *M.*

lyngbyaceus, as the *Lyngbya* form, collected during November, 1968 and June, 1969 from tide pools at the Nahant Town Wharf, were consistently uniform in their dimensions, trichomes 17 μ wide and filaments to 26 μ wide. However, pigmentation of these trichomes was variable, the plants appearing either greenish-blue, yellow, or yellow-brown.

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TRILLIUM PERSISTENS (LILIACEAE), A NEW PEDICELLATE-FLOWERED SPECIES FROM NORTHEASTERN GEORGIA AND ADJACENT NORTH CAROLINA

WILBUR H. DUNCAN, JOHN F. GARST, GEORGE A. NEECE

The first evidence that this new species of pedicellate-flowered *Trillium* existed was the discovery of fruiting specimens by the senior author in Tallulah Gorge, Habersham Co., Ga., on 6 July 1950 (*Duncan* 11, 245). These specimens did not seem to belong to any described species and were finally filed with other miscellaneous "problem" specimens to be sent to persons specializing in the taxa involved. Some of the *Trillium* specimens were sent to Vanderbilt University for naming in 1966 and were identified as *T. catesbaei* Ell. In 1969 two mounted duplicate plants were identified as *T. catesbaei* by Robert G. Johnson (WVA) who had requested *Trillium* specimens for study. These determinations emphasize the similarity of many individuals of the two species when they are not in flower.

When they are flowering, they are obviously distinct. The first flowering specimens were found by Edna Garst on 28 March 1970 along Battle Creek in Oconee Co., South Carolina. On 12 April 1970 the junior authors decided that the *Trillium* was an unusual species, collected specimens with withered corollas from the Battle Creek colony, and brought them in for identification. Comparisons were made of these specimens with the several duplicate fruiting specimens that had been retained. This convinced us that they were conspecific and a new species. Additional specimens with withered corollas were collected by Neece and Garst from a second Habersham Co. locality on 24 April 1970. After observing many hundreds of freshly flowering specimens on 23 March 1971, and making needed measurements, the following description and accompanying text were prepared.

Trillium persistens Duncan, sp. nov.

Herba perennis, glabra. Scapi erecti, 12-25 cm longi.

Bracteae sessiles vel rarenter petiolo alato ad 2 mm longo, lanceolatae ad ovatae, 16-33 mm latae, ad apices acuminati vel raro acuti. Pedunculi arcuati ad erectiusculi, 12-33 mm longi. Sepala acuta, leviter expansa, 13-23 mm longa. Petala erectiscula versus basem et expansa versus apicem, 21-33 mm longa, 5-9 mm lata. Stamina recta, 9.5-13.8 mm longa, antheris introrsis. Ovarium leviter obovatum, acute sexangulum, stylo 2-6 mm longo. Semina circa 2 mm lata et 3.5-4.0 mm longa, minute undulata.

Plants are glabrous perennial herbs. When the flowers are fully opened, the *scapes* are erect, glabrous, 12-25 cm long, 2.5-4.5 times as long as bracts. *Bracts* sessile to very short stalked (to 2 mm long and winged), 3(5)-veined, lanceolate to ovate 16-33 mm wide, 31-95 mm long, 1.9-3.5 times as long as wide, the length 1.3-1.7 times the distance from the tip to the widest part, apices acuminate or rarely acute, the bases acute to obtuse, evenly green in color. *Flowers* above the bracts, on peduncles 12-34 mm long, one fourth to one-half as long as the bracts; peduncles arched to nearly erect (especially with age); the flowers at an angle to the peduncle or in a line with it, thus drooping to nearly erect. *Sepals* slightly outwardly curved, slightly divergent, 3(5)-veined, narrowly elliptic to narrowly ovate, 13-23 mm long, 4-6 mm wide, 3.2-4.9 times as long as wide, apices acute (rarely nearly obtuse) and finely cusped. *Petals* nearly erect towards base and spreading towards the tips, 3-veined, entire margined, undulate surfaced, nearly linear to narrowly elliptic, 21-33 mm long, 5-9 mm wide, 3.0-6.4 times as long as wide, apices acute (rarely nearly obtuse), tapered to a base about 1.7 mm wide, white, later becoming light reddish-purple except at the base, the base remaining white or nearly so. *Stamens* straight or nearly so, 9.5-13.8 mm long, erect to slightly divergent; *filaments* 0.7 mm wide, 4.8-6.0 mm long, 1.8 mm shorter to 0.2 mm longer than the anthers; *anthers* introrse, 4.6-7.8 mm long; *pollen* yellow; *connectives* barely prolonged (to 0.2 mm) and rounded at apex. Gynoecium height at tops of anthers to 4.3 mm beyond; *ovulary* slightly obovate, 2.8-5.5 mm long, sharply 6-angled; *styles* 2.0-6.0 mm long;

stigmas 3.0-7.5 mm long, 2 mm shorter to 2 mm longer than the ovulary, nearly straight to divergent at tips (especially with age). *Seeds* minutely undulate, about 2 mm wide and 3.5-4.0 mm long.

TYPE: *Duncan* 23548 with Garst and Neece. Rooted in well-decomposed litter and/or loose loam. With little other herbaceous growth under scattered *Rhododendron maximum* plants in open deciduous woods on a south-facing slope of Tallulah Gorge, Rabun Co., Georgia, 23 March 1971. HOLOTYPE: US; ISOTYPES: F, GA, GH, NY, VDB.

Trillium persistens individuals, although occurring in the cool Blue Ridge area, flower earlier than those of most species; and yet remain alive above ground until late summer, after other species have died back. Live individuals were found on 12 September (Duncan 23462 with Garst) when individuals of other *Trillium* species in the area were dead above ground. The specific epithet was chosen because of this characteristic.

Distribution: In deciduous or conifer-deciduous woods of ravines or gorges, under or near *Rhododendron maximum* L. or *R. minus* Michx., rooted in well-decomposed litter and/or loose loam. Rabun and Habersham Cos., Georgia; and Oconee Co., South Carolina. All known populations are within four miles of each other and in the Tallulah-Tugaloo River system.

Additional specimens: GEORGIA: Rabun Co., *Duncan* 23547 with Neece and Garst, 23 March 1971 (In flower). Under *R. maximum* in deciduous woods in small ravine near top of Tallulah Gorge and ESE of dam to Tallulah Falls Lake. Elev. about 1500 ft. Habersham Co., *Duncan* 11245, 6 July 1950 (In fruit). Rich, mesic, steep slopes in deciduous woods near bottom of Tallulah Gorge. Elev. about 980 ft. *Neece & Garst*, 24 April 1970 (With withered petals). Under or near *R. maximum* plants on terrace and slopes along Moccasin Creek from edge of Yonah Lake at about 750′ elev. to about 900 ft. *Duncan* 23462 with Garst, 12 September 1970 (Fruits dehisced). Between scattered *R. maximum* plants in forest on north facing slope about 50 feet above Moccasin Creek and 0.1 mile from Yonah Lake. Elev. about 830 ft. *Duncan* 23549 with Garst and Neece, 23 March 1971 (In flower). Under scattered *R. maximum* plants on S side of Tallulah Gorge. Elev. about 980 ft. SOUTH CAROLINA: Oconee Co., *Garst*, 12 April 1970 (With withered petals). Under *R. maximum* on wooded

terrace in steep ravine; Battle Creek, about 1/3 mile from Lake Yonah. Elev. about 850 ft.

Trillium persistens seems related to *T. pusillum* Michx., *T. catesbaei*, and *T. nivale* Riddell. They form a group having a prominent common style, and each is similar to one or more of the others in a number of characters. When flowers are fully developed, *T. pusillum* may be separated by its obtuse bracts, sepals which are obtuse and horizontally spreading or nearly so, and the ovate and obscurely angled ovary; *T. catesbaei* by its ovate to elliptic and petioled (3-12 mm) bracts, sepals that are 20-40 mm long and reflexed or curled, petals that are recurved and 30-55 mm long and 18-30 mm wide, stamens that are curved and 16-26 mm long, and wider filaments; and *T. nivale* by its oval to ovate and obtuse or rarely acute and distinctly petioled (5-10 mm) bracts, and its round 3-lobed ovary. Before flowers are fully opened some plants are difficult to place. However, when differences in geography and the "arrival of spring" are considered, *T. pusillum* and *T. catesbaei* are later flowering. *Trillium persistens* also resembles some individuals of *T. grandiflorum* (Michx.) Salisb. in early flowering stage. The latter species also has straight anthers and a style (though short — to one mm) but may be separated by its shorter style, wider bracts and petals, and ovate ovary. Of the four other species probably only *T. catesbaei* and *T. grandiflorum* are sympatric with *T. persistens*. *T. pusillum* may occur nearby in northwestern South Carolina (Gates, 1917[1]).

Trillium persistens does not occur in large clusters, but as scattered individuals or clusters of less than ten. A two hour search by the junior authors along Moccasin Creek (Habersham Co., Ga.) led to the discovery of only 120 plants along a 0.2 mi stretch beginning at Yonah Lake. Plants are no denser up Battle Creek (Oconee Co., S.C.), but were found as scattered individuals to an elevation of 1200 feet. In Tallulah Gorge (Habersham and Rabun Cos., Ga.) individuals were also mostly scattered but they

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[1]GATES, R. R. A systematic study of the North American genus *Trillium*, its variability, etc. Ann. Mo. Bot. Gard. 4: 43-92. 1917.

were distributed over a much larger area and to about 1500 feet elevation.

Along the two creeks *T. persistens* occurs under or very near *Rhododendron maximum*. It is often associated with *Medeola virginica* L. Two other Trilliums, *T. catesbaei* and *T. cuneatum* Raf., were seen along both creeks and *T. discolor* abundantly along Battle Creek. The forest along the creeks is characterized by *Tsuga canadensis* (L.) Carr., *Fagus grandifolia* Ehrh., *Liriodendron tulipifera* L., *Tilia heterophylla* Vent., *Betula lenta* L., *Magnolia fraseri* Walt., *Acer rubrum* L., and *Quercus*.

In 1970 and 1971 *T. persistens* in its native habitats began flowering around 20 March. Some flowers were withering by the first of April and practically all, if not all, by the middle of April. Flowering time may be more meaningful when compared to those of other species. *Erythronium* begins flowering earlier and is concluding flowering as *T. persistens* is beginning; *Viola hastata* Michx., *Epigaea repens* L., and *Hepatica acutiloba* DC. flower at about the same time; and *Trillium discolor* Wray begins about the time many flowers of *T. persistens* are withering. At Athens, Georgia, a transplanted plant of *T. persistens* flowered 15 March 1971 while native plants of *T. catesbaei* and transplants of *T. grandiflorum* began flowering over one month later.

Pollen from one plant of *T. persistens* was stained in aniline-blue lactophenol for 24 hours. All 314 grains examined were well stained. Thirty grains varied in size from 30-37 μ and averaged 32.8 μ.

We wish to thank Mr. Caywood Chapman for examining pollen, and Drs. Robert Kral and R. B. Channell of Vanderbilt University, Dr. Robert Wilbur of Duke University, and Dr. James Hardin of North Carolina State University for allowing specimens under their care to be examined for this study.

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VASCULAR FLORA OF OSSIPEE LAKE, NEW HAMPSHIRE AND ITS SHORELINE

C. Barre Hellquist

Ossipee Lake, occupying 3091 acres in the towns of Ossipee, Freedom, and Effingham, County of Carroll, is the eighth largest lake in the State of New Hampshire. It is in the Saco River watershed with all water flowing into the Saco River through the Ossipee River. The lake has three bays — Broad, Leavitt and Berry Bays — associated with it. The elevation of the lake is 406 feet and it has a maximum depth of 61 feet. The greatest depth in the bays is 72 feet in Broad Bay. Newell (1960) in extensive studies reports the pH range of the lake between 6.0 and 6.4. The akalinity, Methyl Orange ppm., ranged between 6 and 11. This author has observed water temperatures along the lake shore to range from 70° - 80° during the summer.

Newell (1960) notes 600 acres of shoal at the southeast end of the lake. This area has a maximum depth of approximately eight feet. The shores are 94% wooded, 5% swampy, and 1% meadow. The bottom is 35% muck, 15% rock, and 50% sand.

Emergent and submerged vegetation was reported as scant (Newell, 1960). Observations by this author confirm this for most of the lake but where emergent vegetation is common (Pine River, Meadow Cove and other isolated coves) there is abundant submerged and floating vegetation.

Sampling was conducted at Ossipee Lake and its tributaries, including Pine River to Route 25, Bearcamp River to Route 16, Branch Brook, Hoyt Brook and the Danforth Ponds. All of the mentioned rivers are inlets to the lake. Observations and collections were made along the shores and in the water. The main areas where studies were made are indicated on the accompanying map. The collection period was the summer and autumn of the years 1968-1970. Vouchers have been deposited in the author's personal herbarium and various specimens have also been deposited in

Figure 1. Map of Ossipee Lake and tributaries showing sites of collections.

the Boston State College Herbarium and the University of New Hampshire Herbarium.

Station 1 is located on the south shore of Ossipee Lake along the stretch of shoreline known as Long Sands. Much of this tract is to be developed by the State of New Hampshire for a future state park. This area consists of a fine white sand on the shore and in the water. Sedges and reeds are prevalent. One interesting phenomenon along this south shore is the occurrence of a small sphagnum peat area.

Station 2 is at the mouth of the Pine River. The shore is much the same as the south side of the lake. There is a variance in temperature of approximately 15°F between the lake and the river. The vegetation of this area is mainly composed of submerged and floating aquatics.

Pine River is a deep, cold, slowly flowing river with wooded shores. Going south on the river toward New Hampshire Route 25 is the location of Station 3. At the river bends there are sandy shore areas on the inside of the turns where emergent aquatics are found.

Two stations are located on the western shore of the lake. Station 4 is at the Meadow — Deer Cove area. The shore is sandy with many sedges and rushes growing along the lake margin. This side of the lake is deeper; thus the floral zone does not extend as far out into the lake as other sites. A small stream flows into the lake at the point between the two coves producing a swampy area. At the western end of Meadow Cove is a large flooded meadow.

Station 5 is at the northwestern end of the lake near the mouth of Branch Brook. The shoreline is composed of sedges growing in a sandy environment. Submerged vegetation is not common in this area.

The Bearcamp River near New Hampshire Route 16 is Station 6. This area is easily reached by boat from the lake. The river was rerouted at Route 16 so a backwater has resulted. The location is very swampy and much silt has filled in the backwater. The rerouted river is shallow, flows slowly, and has a sandy bottom. Water temperature varies considerably. The river is approximately 10° - 15°F colder than the backwater. Emergent and submerged aquatics are very common in the stagnant area. Along the river edge submerged plants are common.

The northeastern portion of Ossipee Lake is subjected to much wind and wave action. The shore is basically rocky without any sandy beaches. Aquatics are not common except at one shallow area; therefore no station was established in this section of the lake.

Further south, Station 7 was located at the area known as Pauli Point. This area consists of the large shoal area in the lake and the protected sandy shore facing south from Pauli Point. Much of this area has since been destroyed by the construction of a campground.

One of the most productive areas for pond weeds is Station 8, located at the mouth of the channel to Broad Bay.

The water is approximately six to eight feet deep with a strong current. Plants are particularly abundant where the water is two to six feet deep.

The channel from the lake to Broad Bay has many small coves. Pickerel Cove is sample Station 9. This cove and the one to the west comprise the sample area. The shore is sandy and also has a damp grassy environment. The bottom is a combination of sand and mud. Probably the greatest variety of plants is to be found here.

Further down the channel sampling was conducted at Station 10. The shore area is sandy. This region was disturbed when bulldozing once occurred for houselots. The sand was pushed into the water here, changing the habitat from a wooded area.

The area at the southwestern end of Broad Bay is Station 11. Deep water and shoal areas combine to make this an interesting habitat for submerged and floating plants.

The north end of Broad Bay including the mouth of the river flowing from lower Danforth Pond or Bay is Station 12. The shoreline is comprised of both wooded and sandy areas. Along the shore are many emergent plants and sedges, while submerged aquatics are common in the water. This area is occupied by Bayview Marina, so plants here are subjected to greater exposure to oil and gasoline.

The next two areas are in Danforth Pond (or Danforth Bay as it is sometimes referred to) and Hoyt Brook. Hoyt Brook flows between the three ponds and Broad Bay. Station 13 was situated on the brook between middle and upper Danforth Ponds. The stream is shallow at the southern end, while it ranges up to six feet in depth above the beaver dam. Water flow is slow and the water temeprature is high. The river is clogged with submerged and floating vegetation. The floating plants are found mainly along the periphery of the stream while submerged plants are in the middle of the stream as well as on the periphery.

Upper Danforth Pond (Goodwin Pond) is the site of the last collection area (Station 14) in this tributary. This area is at the northern end where a small stream flows into the pond. The water is approximately 15° - 20°F colder in

the stream than in the pond. The vegetation was very abundant in all forms.

Station 15 is located in Leavitt Bay. It is at the outlet of the bay leading to the channel which flows into Berry Bay. At this station only deep water aquatics were collected. At the other end of the channel, at the south end of Berry Bay, Station 16 is located. Only deep water specimens were observed here, also.

The north end of Berry Bay near the mouth of Square Brook is the final check point (Station 17). Collecting here was done basically in the shallow water along the shore and on the sandy shore.

Many plants are not mentioned as occurring at places where they, in fact, do occur. This is due to the fact that they may have been so common in the lake as a whole that no particular attention was paid to them in the collecting and observation.

Two plants found at Ossipee Lake have been reported only at this location in the State of New Hampshire. These are *Proserpinaca pectinata* Lam. (Seymour, 1966) and *Rhynchospora capillacea* Torr. (Seymour, 1963). *Proserpinaca pectinata* Lam. is found on the south shore at Station 1 in shallow water approximately six inches deep. It is also found in the damp sphagnum area at the same station. *Rhynchospora capillacea* Torr. was reported from Berry Bay but was not in a study area and was not found.

Seymour (1963) reported *Potamogeton nodosus* Poir. in the area of the Pine River mouth in association with *Potamogeton gramineus* L. This species was extensively searched for, but to no avail. *Potamogeton gramineus* var. *maximus* Morong was found in association with *Potamogeton pulcher* Tuckerm., *Potamogeton epihydrus* Raf. var. *Nuttallii* (C. & S.) Fern. and *Potamogeton natans* L.

Fassett (1966) was used as the criterion for the identification of the aquatics. Some plants are included in this survey which Fassett does not consider aquatics. These are included because they were growing along with the aquatics. In the following list, plants referred to as emergent are found at least part of the year partially in the

water. During the late summer the lake level lowers, so many of these plants are out of the water. Submerged plants are found below the water surface. Floating plants have part of the plant floating on the surface.

Nomenclature used is that of Fernald, (1950). The assistance of Dr. Albion Hodgdon of the University of New Hampshire for identfication of many of the grasses, sedges and rushes is gratefully acknowledged.

Isoetes Tuckermani A. Br. — Station 4[1] — submerged, found floating along western shore where it had been uprooted.

Osmunda regalis L. — 1, 3, 13 — emergent, on sandy shore and damp river edges.

Sparganium angustifolium Michx. — 4 — submerged, floating in quiet water, probably more common than observed.

S. americanum Nutt. — 6, 9, 13 — emergent, floating, along sandy and muddy margins.

Potamogeton Robbinsii Oakes — 11, 13, 14 — submerged, specimens found were floating loose just under the surface.

P. Berchtoldii Fieber var. *tenuissimus* (Mert. & Koch) Fern. — 3, 9 — submerged, in slow backwater of rivers and coves.

P. Spirillus Tuckerm. — 3, 6, 12, 13 — submerged, floating, common, usually along shallow shores in water up to four feet.

P. capillaceus Poir. — 3, 12, 13 — submerged, in shallow water.

P. epihydrus Raf. var. *Nuttallii* (C. & S.) Fern. — 2, 3, 8, 11, 13 — submerged, floating, common, in deep water.

P. amplifolius Tuckerm. — 2, 11, 13, 14 — submerged, floating, in slow current.

P. pulcher Tuckerm. — 2, 7, 8, 15 — submerged, floating, common in deep areas near river mouths.

P. gramineus L. var. *gramineus* — 2, 3, 8, 15, 16 — submerged, floating, common in deep water.

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[1]Stations are cited by number (see text and map).

P. gramineus L. var. *maximus* Morong — 3 — submerged, floating, in deep water.

P. gramineus L. var. *myriophyllus* Robbins — 2, 3, 4, 12 — submerged, floating, found along shallow sandy margins.

P. natans L. — 2, 3, 9, 11, 13 — submerged, floating, common in deep areas of lake and rivers.

P. Oakesianus Robbins — 2, 3, 4, 6 — submerged, floating, shallow areas along shore.

Najas flexilis (Willd.) Rostk. & Schmidt — 2, 9, 12, 13 — submerged, in rivers and lake.

Alisma trivale Pursh — 6 — emergent, rare, moist sandy shore.

Sagittaria graminea Michx. — 1, 9, 12 — submerged, emergent, common in shallow muddy areas.

S. latifolia Willd. forma *diversifolia* (Engelm.) Robinson — 6 — emergent, on river margin.

S. latifolia Willd. forma *hastata* (Pursh) Robins. — 3 — emergent, on sandy margin.

S. latifolia Willd. forma *gracilis* (Pursh) Robins. — 4, 6, 9, 13 — emergent, common, along sandy margins among rushes and sedges.

S. latifolia Willd. var. *obtusa* (Muhl.) Wieg. — 4 — emergent, common on shore of Station 4.

S. cuneata Sheldon — 6 — emergent, rare, on muddy shore.

Elodea Nuttallii (Planch.) St. John — 14 — floating, not abundant.

Calamogrostris canadensis (Michx.) Nutt. — 1, 2, 3 — emergent, on lake margin.

Panicum virgatum L. var. *spissum* Linder — 1 — emergent, along sandy shores often in dry as well as damp areas.

Cyperus dentatus Torr. — 9, 10, 12 — emergent, damp and dry margins.

C. strigosus L. — 10 — emergent damp and dry margins.

Dulichium arundinaceum (L.) Britt. — 1, 2, 4, 5, 7, 12 — emergent, common, found along sandy shores in conjunction with sedges and rushes.

Eleocharis acicularis (l.) R. & S. — 13, 14, 17 — submerged, common on muddy bottom.

E. obtusa (Willd.) Schultes — 6 — emergent, along sandy shore.

E. Smallii Britt. — 9 — emergent, along channel margin.

Scirpus Smithii Gray — 6 — emergent, rare, along sandy margin.

S. subterminalis Torr. — 4, 17 — submerged, river, lake bottom.

S. americanus Pers. — 1, 4 — emergent, on sandy margin.

S. atriovirens Willd. — 12 — emergent, on dry and damp shore.

S. Peckii Britt — 4 — emergent, rare, along sandy margin.

S. cyperinus L. forma *Andrewsii* (Fern.) Carpenter — 12 — emergent, damp shore.

S. cyperinus L. var. *pelius* Fern. — 1 — emergent, found among sedges and rushes.

Rhynchospora capitellata (Michx.) Vahl. — 12 — emergent, among sedges.

R. alba (L.) Vahl. — 12 — emergent, associated with sedges and rushes.

Cladium mariscoides (Muhl.) Torr. — 1, 4, 7 — emergent, common on south end of lake at Station 1.

Carex crinita Lam. — 10 — emergent, on dry sandy shore.

C. lurida Wahlenb. — 12 — emergent, on sandy margins.

C. rostrata Stokes — 2, 3 — emergent, in muddy meadows.

C. rostrata Stokes var. *utriculata* (Batt.) Bailey — 12 — emergent, on sandy margin.

C. oligosperma Michx. — 1 — emergent, sandy lake margins.

Peltandra virginica (L.) Schott & Endl. — 13 — emergent, common along muddy shore of Station 13.

Xyris caroliniana Walt. — 1, 4, 9 — emergent, common, with rushes and sedges on sandy shores.

X. montana Ries. — 1 — emergent, rare, lake margin among sedges.

Eriocaulon septangulare With. — 1, 4, 9 — emergent, submerged, common, along shore it is small, in deep water up to six feet in height.

Pontedaria cordata L. var. *cordata* — 1, 4, 7, 10, 12, 13, 14 — emergent, common along shore in shallow water.

P. cordata L. forma *angustifolium* (Pursh) Solms — 1 — emergent, in shallow water.

P. cordata L. forma *taenia* Fassett — 1, 4 — submerged, in shallow water.

Juncus canadensis J. Gay — 1, 9 — emergent, on sandy margin.

J. militaris Bigel. — 1, 4 — emergent, along sandy shore.

J. pelocarpus Meg. — 4, 9, 12 — emergent, in shallow water and on sandy shore.

Iris versicolor L. — 1 — emergent, on sandy shores.

Pogonia ophioglossoides (L.) Ker. — 1 — emergent, although not considered an aquatic, this bog plant was common in the small sphagnum area along the south shore lake margin.

Myrica Gale L. — 9, 10, 13, 14 — emergent, common, along lake and river edges often overhanging the water.

Polygonum amphibium L.[2] — 3 — floating, along muddy shores, often overhanging water.

P. amphibium L. forma *terrestre* (Leers) Blake — 2, 3 — emergent, in damp meadow along river shore.

P. coccineum Muhl. forma *natans* (Wieg.) Stanford — 3, 5 — floating, along muddy shore at Station 3 and in sand at Station 5.

P. hydropiperoides Michx. — 2, 13, 14 — submerged, floating emergent, along river edges and river bottoms in moving water.

P. sagittatum L. — 4 — emergent, not considered aquatic but found on sandy shore with other aquatics.

Ceratophyllum demersum L. — 13, 14 — submerged, in shallow, flowing water.

C. echinatum Gray — 3 — submerged, on muddy bottom in standing water.

Nuphar microphyllum (Pers.) Fern. — 2, 4 — submerged, floating, uncommon.

N. variegatum Engelm. — 1, 2, 4, 5, 7, 9, 11, 13, 14, 17 —

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[2]Mitchell (1968) considers *Polygonum coccineum* Muhl. and *P. amphibium* L. as the same species and has retained the name *P. amphibium* L.

submerged, floating very common, in one to six feet of water.

N. advena (Ait.) Ait. f. — near 4 — emergent, rare in muddy cove north of Bearcamp River in lake.

Nymphaea odorata Ait. — 1, 2, 3, 4, 5, 7, 9, 11, 13, 14, 17 — submerged, floating, very common, in one to six feet of water.

Brasenia Schreberi Gmel. — 4, 13, 14 — floating, in slow flowing water and protected areas.

Ranunculus trichophyllus Chaix — 3, 4 — submerged, in cold flowing water at Station 3 and on lake bottom in four feet of water at Station 4.

R. reptans L. — 1, 6, 17 — emergent, creeping along sand among reeds and sedges.

R. reptans L. var. *ovalis* (Bigel.) T. & G. — 13, 17 — emergent, along sandy margins.

Subularia aquatica L. — 4, 17 — submerged, uncommon, along sandy shore in one to two feet of water.

Cardamine pensylvanica Muhl. — 2, 13 — submerged, in slow flowing water.

Drosera intermedia Hayne — 1 — emergent, along margin with sedges and in sphagnum area.

Potentilla palustris (L.) Scop. — 2 — emergent, trailing into water from river bank.

Callitriche verna L. — 2, 3 — submerged, floating, in cold flowing water up to four feet in depth.

Hypericum punctatum Lam. — 1, 4 — emergent, along sandy margins.

H. ellipticum Hook. — 2, 6, 9, 12 — emergent, common, along sandy margins.

H. boreale (Britt.) Bickn. — 1 — emergent, along sandy margins.

H. boreale (Britt.) Bickn. forma *callitrichoides* Fassett — 2, 6, 12 — submerged, in sandy and muddy margins.

H. canadense L. — 9, 12 — emergent, along sandy margins.

H. virginicum L. — 1, 2, 4, 9 — emergent, common, on sandy shores and shallow water.

Elatine minima (Nutt.) Fisch. & Mey. — 4, 7, 12 — submerged, on sandy bottom in one to two feet of water.

Viola lanceolata L. — 9 — emergent, on grassy shore.

Rhexia virginica L. — 1 — emergent, on sandy margin among sedges.

Ludwigia palustris (L.) Ell. var. *americana* (D.C.) Fern. & Grisc. — 13 — submerged, on muddy bottom on slow flowing warm water.

L. palustris (L.) Ell. var. *americana* (D.C.) Fern. & Grisc. forma *elongata* — 14 — submerged, floating, in cold water.

Myriophyllum alternifolium D.C. — 14 — submerged, specimens found floating along surface after breaking loose.

M. Farwellii Morong — 13 — submerged, floating, some specimens floating just under surface along shore.

M. humile (Raf.) Morong forma *capillaceum* (Torr.) Fern. — 13 — on muddy river bottom.

M. tenellum Bigel. — 1 — submerged in deep water.

Proserpinaca palustris L. — 4 — submerged, rare on muddy bottom in swampy area between Meadow and Deer Cove.

P. pectinata Lam. — 1 — submerged, emergent, uncommon, with sphagnum moss and submerged along lake margin in six inches of water.

Sium suave Walt. — 3, 7, 13 — emergent, along damp shores and meadows.

S. suave Walt. forma *Carsoni* (Durand) Fassett — 2, 13, 14 — submerged, common in slow flowing rivers with muddy bottoms.

S. suave Walt. forma *fasciculatum* Fassett — 16 —submerged, rare, in shallow water in sand.

Chamaedaphne calyculata (L.) Moench — 4 — emergent, uncommon, along shore in sand.

Vaccinium macrocarpon Ait. — 1, 2, 4, 9, 16 — emergent, common, lake margin.

Lysimachia terrestris (L.) B.S.P. — 1, 2, 7, 12 — emergent, common, among sedges on lake margin.

L. ciliata L. — 6 — emergent, rare on damp shore.

Nymphoides cordata (Ell.) Fern. — 1, 2, 4, 7, 9, 11, 13, 15 — submerged, floating, usually in deep water up to eight feet.

Asclepias incarnata L. — 3, 13, 14 — emergent, along river and lake margins.

Scutellaria lateriflora L. — 2, 7, 12 — emergent, among grasses along river edge and along sandy shore.

S. epilobiifolia A. Hamilton — 1, 2, 4 — emergent, among grasses along river edge and along sandy shore.

Lycopus uniflorus Michx. — 4, 6 — emergent, along sandy margin.

L. americanus Muhl. — 5, 6 — emergent, along sandy margin.

Mentha spicata L. — 5 — emergent, rare, along river edge.

M. arvensis L. var. *arvensis* — 4, 6 — emergent, on sandy and muddy shore.

M. arvensis L. var. *villosa* (Benth.) S. R. Stewart — 6 — emergent, on muddy shore.

Chelone glabra L. var. *glabra* — 3, 12, 14 — emergent, along river shores and meadows.

Gratiola aurea Muhl. — 1, 4, 5, 7, 9, 13, 16 — emergent, common, on sandy margins.

G. aurea Muhl. forma *pusilla* Fassett — 1, 4, 5, 9 — submerged, in shallow water.

Lindernia anagallidea (Michx.) Pennell — 12 — emergent, uncommon sandy margin.

Veronica scutellata L. — 2, 12 — emergent, among grasses on sandy margins.

Utricularia purpurea Walt. — 3, 6, 11, 12, 13, 14, 15 — submerged, common, in areas with slow current.

U. inflata Walt. — 11, 12, 13, 14, 15, 16 — submerged, common, in slow current.

U. inflata Walt. var. *minor* Chapm. — 13 — submerged, uncommon, slow flowing water.

U. vulgaris L. — 3, 6, 13, 14 — submerged, in slow current.

U. intermedia Hayne — 6, 13, 14, 17 — submerged, along muddy shores in shallow water.

U. cornuta Michx. — 1, 9 — emergent, sandy margins among sedges.

Cephalanthus occidentalis L. — 2, 4, 6, 12, 13 — emergent, common, on sandy shores and along river edges.

Campanula aparinoides Pursh — 3, 7 — emergent, grassy shores.

Lobelia cardinalis L. — 3 — emergent, uncommon except along Branch Brook above station where it was abundant. Found on river shore.

L. Dortmanna L. — 4, 9 — emergent, submerged, along sandy margin.

Eupatorium dubium Willd. — 6 — emergent, on sandy shore.

E. maculatum L. — 6 — emergent, on sandy shore.

E. perfoliatum L. — 4, 7 — emergent, along lake margin among sedges.

Solidago graminifolia (L.) Salisb. — 2, 4 — emergent, along lake margin.

S. tenuifolia Pursh — 1, 2, 4 — emergent, along lake margin.

Aster Tradescanti L. — 2, 6, 7 — emergent, along sandy margin.

A. nemoralis Ait. — 10 — emergent, river margin.

A. umbellatus L. — 6, 7 — emergent, lake margin.

Bidens frondosa var. *pallida* Wieg. — 6 — emergent, muddy meadow.

Megalodonta Beckii (Torr.) Greene — 13, 14 — submerged, in slow current and muddy margins.

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BENTHIC SALT MARSH ALGAE AT IPSWICH, MASSACHUSETTS[1]

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This paper is the first of a two-part study of the attached algae of the Ipswich salt marsh. Here, emphasis is placed on the occurrence, periodicity, and morphology of the benthic algae. A second paper will describe in detail the ecology of the marsh algae at Ipswich.

In previous botanical investigations of salt marshes, studies of seed plants far exceed those of other plant groups. For the New England area we can refer to Chapman's (1939, 1940) studies of the Saugus (Massachusetts) marsh in which he emphasizes flowering plants. More recently, Blum (1968) demonstrated the interrelationships between salt marsh Spartinas and their associated benthic algae. Summaries of the few papers which deal with the New England salt marsh flowering plants are presented by both Chapman and Blum.

On the other hand, considerable attention has been focused on the extensive marshes of the southern and southeastern Atlantic coast. Pomeroy (1958, 1959), Schelske & Odum (1961), and Odum (1961) contributed much with respect to our knowledge of community structure and overall productivity of the southern tidal marshes. Similar studies in orientation and details have not been attempted in New England salt marshes.

Unlike the salt marsh flowering plants, the attached algae of these eco-systems remains a poorly developed focus of research, whether in the Gulf and southeastern United States or in New England. Chapman (1960) summarized the literature dealing specifically with marsh algae, convincingly demonstrating the need for long range studies of these little understood but important plants.

Doubtless, by far the greater number of benthic marine algal species found in New England salt marshes are rep-

[1]Revised portion of a Ph.D. thesis, of senior author, University of Massachusetts.

resented in Taylor (1957). Taylor's treatment, however, presents but a stylized description of these species and the briefest account of their occurrence. The greatest source of omission in this flora lies not with the macroscopic algae, but with the numerous minute forms which can be determined only through careful microscopic examination. Of these forms, the attached chrysophytes and haptophytes undoubtedly contain the largest number of species new to our area and new to science. Nonetheless, Taylor (1957) is our point of departure for phycological literature pertaining to the salt marshes of the northeast.

Salt marshes are low areas immediately landward to a coast or embayment. The seaward portions of the marsh are inundated periodically by full strength seawater, with the more peripheral landward extensions being subject to freshwater inflow. Commonly, marshes are strongly dissected with tidal creeks of varying sizes, which result in a more rapid mixing of marine and freshwater. Thus, the salt marshes are unique, well defined environments characterized by gradients in salinity, temperature, pH, tidal amplitude, and are rarely exposed to waves of any size.

Tidal marshes are deceivingly homogeneous in appearance with respect to their macroscopic vegetation, being dominated by species of *Spartina* (*S. alterniflora* var. *glabra*, *S. patens*, and *S. pectinata*) and various members of the Chenopodiaceae (*Atriplex*, *Suadea*, and *Salicornia*). The *Spartina* grasses are particularly important in that they bind the predominantly loose organic substratum of the marsh, add to this substratum through senescence and decay, and, in part, bring about changes in its composition. The seed plants, however, represent but a small fraction of the total number of marsh plant species, if one includes the attached algae; by far the greater number of species present belong to the algae. Owing to their relatively small size in relation to the flowering plants, the algae are invariably overlooked unless one makes an effort to search them out. Small they may be, but because of their large numbers and frequently sharp seasonality, the marsh sur-

face takes on distinctive and different subtle hues owing largely to the periodicities of these plants.

Salt marshes are of further interest in that their biological features are directly related to and result from the distinctive physical and chemical characteristics of the marsh. The attached alga constitutes a highly appropriate tool of research for the study of biological adaptation to continuous changes of virtually all of the environmental factors present in the marsh. Owing largely to their small size, populations of marsh algae may be grown easily and rapidly in culture. Studies of the control of the initiation, formation, and discharge of sexual and asexual reproductive cells can be achieved using selected taxa of marsh algae. Growth rates and initial development as affected by different degrees or combinations of different environmental factors can be studied *in vivo* and relationships drawn with comparable situations in the natural environment. Moreover, the characteristically sheltered environment of the marsh, unlike that of the open coast or the sublittoral, makes more feasible long lasting experiments under natural conditions which may parallel or supplement experiments under the controlled conditions of the laboratory. We propose that the salt marsh environment and the salt marsh algae offer many opportunities for the phycologists interested in experimental ecological investigations. In our experiences, the salt marsh environment is a fascinating and fruitful area . . . many questions remain to be discovered concerning the marsh biota, and still more remain to be answered.

The conspicuous mud flats and meadow-like expanses of marshland in and surrounding the Ipswich area comprise approximately 10% of the total salt marsh acreage in Massachusetts (Mass. Dept. Nat. Res., 1964). Here, the salt marsh acreage adjacent to the Castle Neck River, Ipswich, Mass., was chosen for an intensive botanical investigation. The Castle Neck River and its system of tidal creeks constitute a true estuarine environment.

Following a 13 month study of the algal vegetation of the Ipswich marsh, 5 stations were selected as representing

a habitat range and, in all probability, close to total algal diversity within the entire marsh system. Collections from these stations were made at a minimum of fortnightly intervals from September, 1963, through December, 1964. Each station was delimited by a line transect 1.5 m wide and of varying length depending on physiognomy of the station.

Positions of the 5 stations chosen for this study are indicated in Fig. 1; a few comments concerning the character of these stations are appropriate: **Station 1:** typically marine, little influenced by freshwater runoff; shoreline a vertical mud bank; substrates of mud, rocks, small stones, and phanerogams. **Station 2:** similar to Station 1, but a

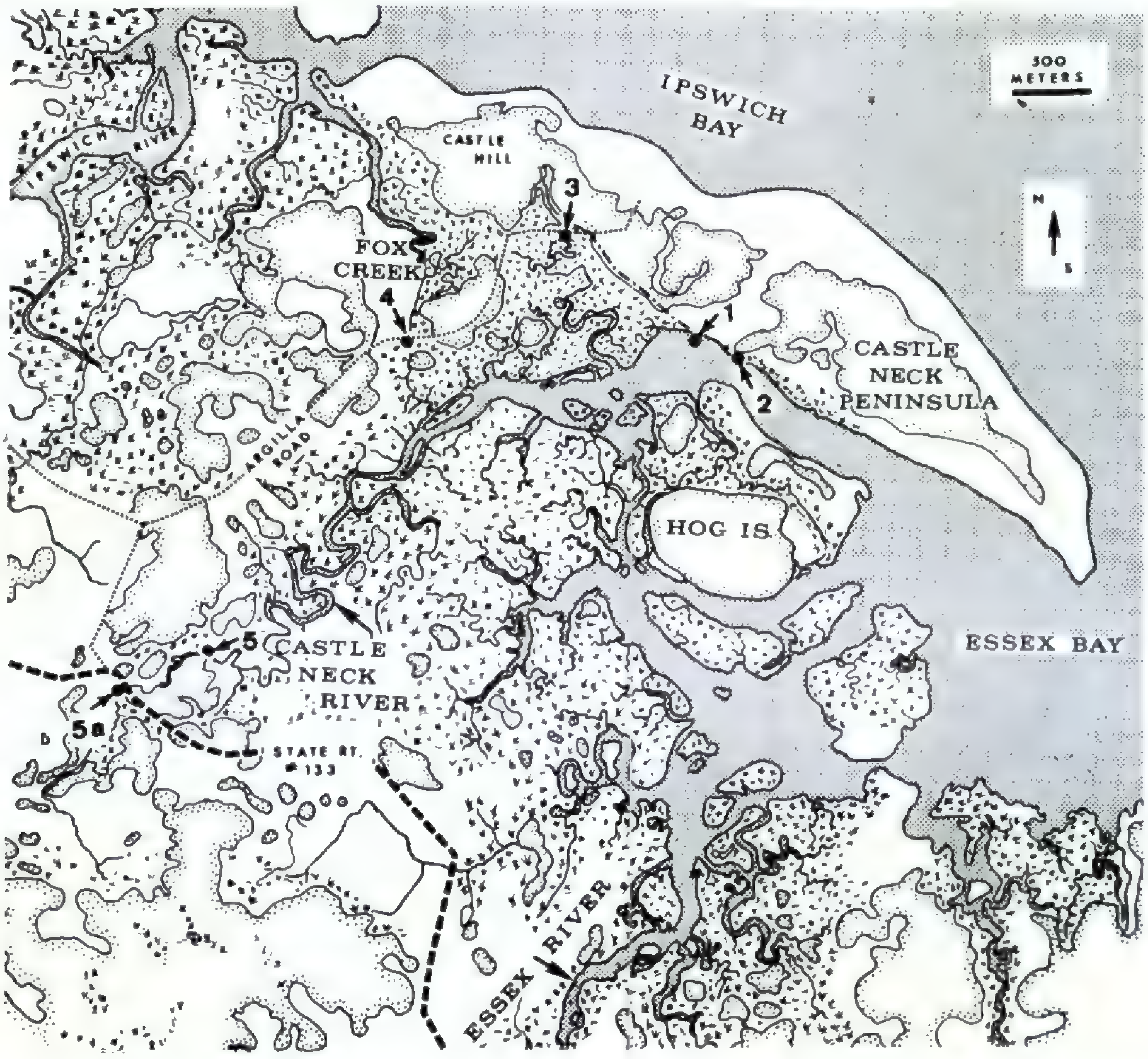

Fig. 1. Location of stations studied at the Ipswich Marsh. Land of highest elevation is enclosed by solid lines and stipple.

more gently sloping shore; substrates predominantly rocks, small stones, *Modiolus demissa*, and phanerogams. **Station** 3: tidal ditch outflow 0.3-1 m deep, seasonally influenced by freshwater runoff; substrates of small stones and wood pilings. **Station** 4: sector of a tidal creek beneath a bridge spanning Fox Creek 1.6 klm west of Station 3; 1.5 m of water at high spring tides, essentially dry at low water level; deeply shaded; substrates of small stones, shells, and wood pilings. **Station** 5: consists of two substations, 5*a* and 5*b*: Substation 5*a*-transect through a major tidal creek which runs under Northgate Rd. (intersect with State Rt. 133) at the head of the marsh; 0.6 m at high water and a variable cover of freshwater at low tide; substrates of small stones, mud, and the phanerogam *Ruppia maritima*. Substation 5*b*-differs from 5*a* in the prevalence of a mudsilt substrate, continuous deep water [ca. 0.6 m] coverage, and its slow movement of water downstream.

Fortnightly measurements were made of salinity, water temperature, and pH at each station. Because these parameters change continually in an estuarine area, their patterns of seasonal fluctuations and their extremes more accurately characterize each station than do average values. Ranges in salinity, water temperature, and pH are presented in Table I.

Table I. Salinity, Temperature, and pH Ranges

Stations	Salinity Range (0/00)	Temperature Range (°C.)	pH Range
1, 2	18 - 33	-1.5 - 24	7.3 - 8.0
3	3 - 33	-2 - 27	6.7 - 8.0
4	13 - 32	3 - 23	7.2 - 7.8
5, a and b	0 - 27	0 - 25	6.4 - 7.4 (7.6)

The salinity systems of Rochford (1952) and the Venice System (1959) were used to characterize the water mass at each station. All salinity data indicate the station studies encompass a distinctly estuarine environment.

Algal cultures used in this study were grown in petri dishes containing Erd-Schreiber solution (Provasoli, et al., 1957), either full strength or diluted by 1/2 normal seawater depending upon the marine character of the environment from which the plants were collected. Cultures were maintained either at temperatures of 10-11°C or at 14-15°C under constant light; light intensities ranged from 50-200 f.c., as measured by a Weston Illumination Meter Model 756.

Species Tabulation and Comments

There are few papers that pertain strictly to the attached algae of New England tidal marshes; this paucity of information is particularly apparent in any phycological consideration of salt marshes of the Massachusetts coast. Our study tabulates the attached marine algae collected in the Ipswich marsh and also presents morphological, cytological, and life history details of some salt marsh algae which are incompletely understood or which have been unknown. In addition, we have attempted to make evident a variety of phycological problems which await future research.

CYANOPHYTA[2]

CHROOCOCCALES

Coccochloris stagnina Spreng.
Anacystis dimidiata (Kuetz.) Dr. & D.
Agmenellum quadruplicatum (Menegh.) Breb.

CHAEMOSIPHONALES

Dermocarpa olivaceus Crouan
D. violacea Crouan
D. prasina (Reinsch.) Born. & Thur.

HORMOGONIALES

Oscillatoria amphibia Ag.
O. subuliformis Kuetz.
Spriulina subsalsa Oersted.
S. major Kuetz.
H. glutinosum (Ag.) Gom.
H. holdenii Tilden
Schizothrix calcicola (Ag.) Gom.

[2]Descriptions and ecological data for blue green species have been published previously (Webber, 1967).

Lyngbya aestuarii (Mert.) Lieb.
L. aestuarii var. *ferruginea* Gom.
L. lutea (Ag.) Gom.
L. semiplana (C. Ag.) J. Ag.
Symploca hydenoids Kuetz.
S. atlantica Gom.
S. funicularis Setch. & Gardn.
Hydrocoleum lyngbyaceum Kuetz.
Microcoleus chthonoplastes Thur.
M. tenerrimus Gom.
Nodularia harveyana (Thwaites) Thur.
Anabaena torulosa (Carm.) Lag.
Tolypothrix tenuis Kuetz.
Calothrix confervicola (Roth) Ag.
C. crustacea (Thur.) Fan
Rivularia atra Roth
R. nitida Ag.

CHLOROPHYTA

Systematic treatment of the green algae follows that used by Taylor (1957), with several exceptions. For *Enteromorpha*, reference was made to Bliding (1938, 1944, 1963, 1968); for species of *Cladophora*, van den Hoek's (1963) scheme was adopted; for *Rhizoclonium*, Koster's (1955) revision was followed.

CHLOROCOCCALES

Codiolum gregarium var. *intermedium* (Fosl.) Collins
Endophytic through the year in leaves of *Spartina* grasses and *Glaux maritima*. Station 1.

Chlorochytrium moorei Gardn.
Endophytic in *Enteromorpha flexuosa* ssp. *paradoxa* in December. Station 1.

C. grande Bristol
Abundant in leaves of *Spartina patens* in October. Station 1.

ULOTRICHALES

Ulothrix flacca (Dillw.) Thur. in LeJol.
Attached to wood pilings, marsh grasses, and littoral fuci from December to early May, with zoospores through the winter and spring and isogametes in March. Stations 1, 2.

U. pseudoflacca Wille
Located from January through May mixed with *U. flacca*, zoospores produced through the spring, biflagellate

swarmers not seen. Stations 1-3, most abundant at Station 3.

U. subflaccida Wille

On wood pilings and stones from November through the winter to May, mixed with the two above *Ulothrix* species, only zoospores seen. Stations 1-3.

Pseudendoclonium submarinum (Reinke) Aleem & Schulz.

Collected throughout the year, but most luxuriant during the winter, from supralittoral wood pilings.

Cultures of this species from small clusters of cells yielded highly branched filamentous plants. Zoosporangia (Wille, 1901, figs. 124-126) were found in culture material, as were biflagellate swarmers, but discharge from sporangia was not seen. Fusion of motile cells is still to be described for this species.

Percursaria percursa (C. Ag.) Bory

This species was most abundant along the seaward marsh edge, from October through May, entangled with *Rhizoclonium riparium* in the Spartinetum alternifloretum. Stations 1, 2.

Bliding (1963) demonstrated sexual and asexual motile cells in this species; these were not seen from either field or cultured material of the Ipswich plants.

Capsosiphon fulvescens (C. Ag.) Setch. & Gardn.

At the Ipswich salt marsh, this species is represented by two populations which are morphologically, spatially, and seasonally distinct. Plants 10 cm long by 1 mm wide were collected from an upper littoral marsh depression at Station 1 (April through June), their occurrence coinciding with a salinity range of between 18-30o/oo. By contrast, plants of *C. fulvescens* having a maximum length of 1 cm and a width varying from 24-68 μ (maximum of 90 μ, occurred on small stones at the extreme head of the marsh (Substation 5a, August through December); during this time the salinity ranged from 2-20o/oo.

Capsosiphon fulvescens is clearly a euryhaline species. Do major salinity changes alone or in combination with other environmental factors control its gross morphology

at Ipswich? Or are we, perhaps, dealing with two genetically distinct populations of this species? Waern (1952) and Bliding (1963) also cite *C. fulvescens* as a euryhaline species, but do not make reference to form differences within the populations they studied. Another factor that may have some bearing on the grossly different development of the two populations at Ipswich is the lack of tidal emersion for the plants at Substation 5a and the normally occurring changes in tidal amplitude at Station 1. Additional studies of *C. fulvescens* involving both laboratory and field approaches are required before more can be said about plants of this taxon.

In our cultures, *Capsosiphon fulvescens* plants of both populations formed quadriflagellate zoospores which, after release from the parental cells, grew into erect thalli. On the other hand, Bliding (1963), in addition to finding quadriflagellate zoospores, reported biflagellate swarmers; he was unable to ascertain the function of these biflagellate cells. We have not obtained biflagellate swarmers from the Ipswich plants.

Enteromorpha

The morphological variations assumed by species of *Enteromorpha* in response to environmental conditions in large measure negate the value of growth habit as a diagnostic feature for species determination. Rather, cytological characteristics, such as cell size, shape, pattern of arrangement, plastid morphology, and number of pyrenoids appear to be more stable species criteria.

Because this genus has long been recognized as troublesome, our preliminary species determinations were sent to Dr. Bliding either for confirmation or reassignment; the species determinations given here are essentially those of Bliding.

Immediately below the seaward marsh edge at Station 1 there occurs a distinct band of green vegetation which we refer to as the "Enteromorpha facies" (Fig. 2); the species here include *Enteromorpha ahlneriana*, *E. intestinalis*, *E.*

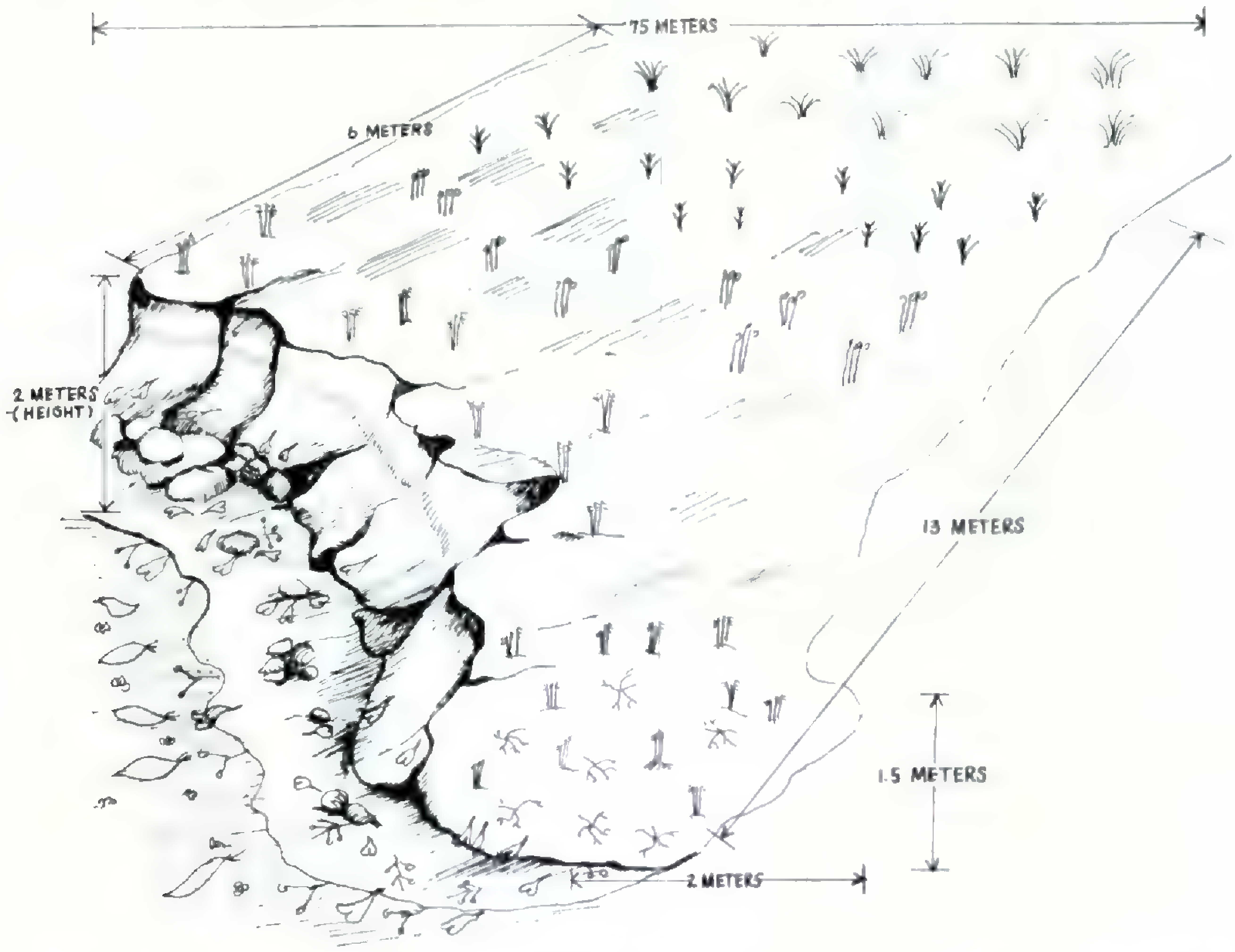

Fig. 2. A shore segment along the Castle Neck River indicating the *Enteromorpha* facies.

flexuosa ssp. *paradoxa*, and *E. prolifera*. By contrast, several other *Enteromorpha* species were located solely in the upper littoral zone, e.g., *E. ahlneriana* type II and *E. flexuosa* type III; still others were restricted to the sublittoral zone, namely *E. ahlneriana* type III, *E. clathrata*, *E. linza* (and var. *oblanceolata*), and *E. flexuosa* (ssp. *flexuosa* and ssp. *pilifera*). *Enteromorpha intestinalis* was the only *Enteromorpha* to be located in both sublittoral and upper littoral regions.

KEY TO ENTEROMORPHA SPECIES

a. Plants unbranched, or with small proliferations from the conspicuous stipe-like lower portion. b.

a. Plants highly branched. c.

  b. Plants hollow throughout, cells commonly in 2's and irregularly placed, one pyrenoid per cell. . . . . *E. intestinalis*

b. Plants with the thallus fused in the mid region so that only the edges and stipe are hollow as seen in cross section, cells in longitudinal and horizontal rows, one pyrenoid per cell. .... *E. linza* var. *linza*
b. Thallus markedly expanded above, a plant of winter and early spring. .... var. *oblanceolata*
c. Plants repeatedly branched, branches tapering to the apex, cells rounded below and irregularly placed, in longitudinal rows above, 3-4 pyrenoids per cell. .... *E. clathrata* I
c. Plants branched, branches not tapering to the apex, cells in longitudinal rows throughout, pyrenoids mostly 1-3. d.
d. Pyrenoids 1 (2) per cell. .... *E. ahlneriana*
d. Pyrenoids mostly 2-4 (5) per cell.
e. Branches multiseriate, tips long and uniseriate, main axis cells with mostly 2-4 pyrenoids. .... *E. flexuosa* ssp. *flexuosa*
e. Branches mostly uniseriate, cells with 1-3 pyrenoids throughout. .... ssp. *paradoxa* III
e. Branches narrow, sharply distinct from the much broader main axis, cells with 3-5 pyrenoids. . . .. ssp. *pilifera*

E. ahlneriana Bliding

Plants to 14 cm long, with or without a distinct main axis, thalli to 1 mm wide, highly branched with branches either long and uniseriate or broad (to 1 mm) and tapering at the base, cells 8.6-18.6 $\mu \times$ 12.4-31 μ, in longitudinal rows, one (rarely two) pyrenoid per cell. One group of plants of this species resembling Bliding's type II occurred throughout the year in the *Enteromorpha* facies. Station 1. A second population resembling Bliding's type III was collected from rocks and shells throughout the summer in the sublittoral. Stations 1 and 2.

E. clathrata (Roth) Grev. type I

Plants to 20 cm long, several orders of branching, main axis to 500 μ wide, branched to 220 μ diameter and ultimately tapering to 12.4-15 μ wide at the tips, cells 14-22 $\mu \times$

11-31 μ, in a longitudinal series, 3-4 pyrenoids per cell. Attached to stones and *Fucus vesiculosus* during the summer in the sublittoral. Stations 1 and 2.

E. intestinalis (L.) Link var. *intestinalis*

Plants unbranched or slightly proliferating at the base, thallus expanded above the stalk-like base, 1 mm to 1 cm wide and to 50 cm long, cells 7.4-15 μ × 12.4-18.6 μ, occasionally to 24.8 μ, cells with rounded to angled walls in surface view and usually grouped in 2's, irregularly arranged, one pyrenoid per cell and the chloroplast not covering the cell face; thallus 19-25 μ thick in cross section with the cells 14.8-17 μ tall.

Two size classes of this species were evident during this study. One population consistently contained relatively small plants (to 7 cm) and collected through the year from the *Enteromorpha* facies. A second size class contained larger plants (to 50 cm) attached to stones and *Ruppia maritima* in Substation 5a and occurred only during the summer. The consistent size disparity between these two populations may be related to salinity differences for maximum growth of *E. intestinalis* at Ipswich appears inversely proportional to salinity levels. A similar relationship of plant size and salinities has been reported by Bliding (1963) for different populations of *E. intestinalis*. In August the *Enteromorpha* plants from Substation 5a released biflagellate, non-fusing swarmers. According to Bliding (1963) such swarmers may represent one half of a sexual strain, or they may function as zoospores, as apparently was the fate of these swarmers from Ipswich.

E. linza (L.) J. Ag. var. *linza*

Plants unbranched, to 1 cm wide and to 18 cm long, thallus blade-like and fused in the mid-region so that only the edges and stalk portions are hollow, as seen in cross section, cells 9-12.4 μ × 8.6-18.6 μ with thick, rounded walls, cells arranged in horizontal and longitudinal rows, one pyrenoid per cell; thallus 49-55 μ thick below and 62-68 μ thick above in cross section with the cells 10-17 μ wide and

31 μ tall; quadriflagellate zoospores released in September. Attached to small stones from June to October in the upper sublittoral. Stations 1 and 2.

var. *oblanceolata* Doty

Plants to 17 cm long, thallus markedly expanded above to 1.5 cm.; the plants 68 μ thick in cross section of the mid region, the cells here 14.8-18.6 μ diameter and 22-27 μ tall. Collected on small stones from February to April in the upper sublittoral. Stations 1 and 2.

E. flexuosa (Wulfen ex Roth) J. Ag. ssp. *flexuosa*

Plants to 35 cm long, highly branched, tips long and uniseriate but branches not markedly tapering, 25-37 μ wide, cells 12.4-15 μ × 12.4-31 μ, in longitudinal rows, 2-4 (5) pyrenoids per cell with 2 most commonly in the smaller branch cells. Attached to stones and *Fucus vesiculosus* during the summer in the sublittoral. Stations 1 and 2.

ssp. *paradoxa* type III (Dillw.) Bliding

Plants to 7 cm long, branches mostly uniseriate or at least with uniseriate tips, cells 12.4-21 μ × 24.8-31 μ, occasionally to 40 μ, cells arranged in horizontal and longitudinal rows, 1-3 pyrenoids per cell. This plant appears to be the *Enteromorpha plumosa* Kuetz. listed in Taylor (1957). Present throughout the year as a component of the *Enteromorpha* facies. Station 1.

ssp. *pilifera* (Kuetz.) Bliding

Plants to 30 cm long, "intestinalis-like" in appearance, narrow branches markedly distinct from the broader main or central axis, cells 12.4-17 μ × 11-24.8 μ, arranged in longitudinal rows but becoming unordered in large plants, the largest cells with angled edges, 4-5 pyrenoids per cell, but 3-4 in cells of the smallest branches. These plants strongly suggest *Enteromorpha prolifera* (Muell.) Ag. in Taylor (1957). Attached to submerged rocks and wood through the summer. Station 3, but occasionally located on stones in the sublittoral, Stations 1 and 2.

Enteromorpha sp.

Several other *Enteromorpha* species were collected from

the Ipswich salt marsh, these rarely and in small quantity. Before accurate species descriptions can be presented, we prefer to have more data from field collections and laboratory cultures. Tentatively, these plants, all recorded from Massachusetts for the first time, are *Enteromorpha prolifera* (Muell.) J. Ag. (ssp. *prolifera* Bliding and ssp. *gullmariensis* Bliding), and *Blidingia minima* Kylin.

Ulvaria oxysperma (Kuetz.) Bliding

Present as small plants (to 5 mm long) at the seaward marsh edge, October through June, Stations 1, 2. Larger plants (to 6 cm long) occurred on wood pilings, September to April, Station 3, and on small stones from September through December. Substation 5a.

Kornmanniana leptoderma (Kjellm.) Bliding

Plants commonly to 7 cm long, epilithic and epiphytic on algae, December to May, Stations 1, 2; epilithic from November to March, Station 4.

Ulva gigantea (Kuetz.) Bliding

Epilithic through the year in the sublittoral, most abundant during the summer. Stations 1, 2.

U. rigida (C. Ag.) Thur.

On submerged rocks and woodwork from June to November, zoospores in September. Station 3.

CLADOPHORALES

Chaetomorpha linum (O. F. Muell.) Kuetz.

Epilithic in the sublittoral through the year. Stations 1, 2.

C. melgonium (Web. & Mohr) Kuetz.

Collected as floating masses washed in among *Chondrus crispus*; doubtful as occurring as attached in the salt marsh. Station 4.

Rhizoclonium riparium (Roth) Harv.

Three forms are described from the Ipswich marsh; all three inhabit the marsh surface throughout the year, extending vertically from the *Spartinetum alternifloretum* landward to *Juncus gerardi*. Stations 1, 2.

f. *riparium* — filaments from 18.6-27 μ dia., rhizoidal

branches generally lacking, but if present, unicellular and short.

f. *validum* Fos. — filaments 31-62 μ dia., with or without rhizoidal branches.

f. *polyrhizum* Rosenv. — differing from f. *validum* by branching of the vegetative filaments, with rhizoids well developed and often multicellular.

R. implexum (Dillw.) Kuetz.

Filaments unbranched, 12.4-13.6 wide μ, cells 2-3 1/2 diameters long, occurring as entangled clumps beneath *Spartina patens.* Station 3.

Cladophora albida (Huds.) Kuetz.

Epilithic in the summer in the sublittoral, Stations 1 and 2, and as old and worn axes in January and September, Station 3.

C. sericea (Huds.) Kuetz.

On mid-littoral mud surfaces through the summer, Station 1, and as old and proliferating axes in tidal wash, Station 4.

The Ipswich plants are comparable with *C. flexuosa* (Muell.) Kuentz. (Söderström, 1963), and also with *C. glaucescens* (Griff.) Harv. and *C. crystallina* (Roth) Kuetz. in Taylor (1957).

C. vagabunda (L.) van den Hoek

Common in a drainage ditch during the summer, reduced to old (perenniating ?) axes in November, Substation 5b; also entangled with other algae, January and August, 1964, Station 3.

The Ipswich plants appear similar to *Cladophora expansa* (Mert.) Kuetz. in Taylor (1957).

C. liniformis Kuetz.

Entangled with other algae during the summer, Station 3, and washed ashore in September, Station 2.

SIPHONALES

Bryopsis plumosa (Huds.) C. Ag.

Attached to submerged rocks and wood from June to late December, the plants observed were always vegetative. Station 3.

Phaeophyta

The systematics of the brown algae essentially follows the treatment used by Taylor (1957), with these exceptions: speciation in *Ectocarpus* follows Rosenvinge & Lund (1941) and Cardinal (1964); Powell's (1957) study is used for *Focus*; for *Laminaria*, see Wilce (1965); treatment of the Dictyosiphonales is after Papenfuss (1947).

ECTOCARPALES

Ectocarpus

The morphology of the plurilocular reproductive structures has been a widely used criterion to aid in determination of *Ectocarpus* species. However, one commonly encounters plurilocular organs whose morphology not only varies broadly within a given species, but also cuts across criteria used for species delineations. Examples of such variations are shown by Rosenvinge & Lund (1941, p. 19-20), Cardinal (1964, figs. 2-3), and in our collections of December, 1962 and those from August, 1963 to January, 1964. Therefore we choose to place less weight on the morphology of the plurilocular organ, thereby recognizing the following taxa from the Ipswich marsh:

E. confervoides var. *confervoides* (Roth) Kjellm.
Epiphytic on *Fucus vesiculosus* through the year, reproductive from October through December. Stations 1, 2.

E. confervoides var. *arcta* (Kuetz.) Kjellm.
Attached to plant debris in the *Enteromorpha* facies, seen only in October and November. Station 1.

E. confervoides var. *siliculosus* (Dillw.) Kjellm.
Epiphytic on coarse algae, April to July, plurilocular in May. Stations 1, 2.

E. confervoides var. *dasycarpus* (Kuck.) Rosenv. & Lund
Epiphytic on *Ruppia maritima* and on small stones, May to December, Substation 5a; epilithic from August through January, Station 3.

The Ipswich plants of this variety are considerably taller (10-12 cm), and have plurilocular organs approxi-

mately twice as wide (30 μ) and 2 1/2 times longer (to 660 μ) than previously reported (Rosenvinge & Lund, 1941; Taylor, 1957; Cardinal, 1964).

Giffordia sandriana (Zanard.) Hamel

Epiphytic on *Fucus vesiculosus* in the sublittoral zone, October and November. Station 2.

Pylaiella littoralis (L.) Kjellm.

At Ipswich, this species exists as two populations. One has plants highly branched, the old filaments wound into cord-like strands, epiphytic on *Fucus vesiculosus* in the sublittoral zone from July through December at Stations 1, 2. A second population consists of plants sparingly branched, with cells narrower and longer than the above, and occurs attached to plant debris in the *Enteromorpha* facies from December to March at Station 1. Plurilocular and unilocular reproductive organs were seen in both populations. Similar populations of *P. littoralis* distinct in morphology, vertical distribution, and seasonal occurrence have been reported from Great Britain (Russell, 1963).

Porterinema fluviatile (Porter) Waern

Epilithic on small stones, April, 1964. Substation 5a. (See Wilce, *et al.* 1970 b).

Ralfsia clavata (Harv. in Hook.) Crouan

Collected throughout the year on rocks in the sublittoral zone, sporangia from August to April. Stations 1-4.

R. verrucosa (Aresch.) J. Ag.

The location, seasonal occurrence, and reproductive periodicity for this species is the same as that for *Ralfsia clavata*.

Petroderma maculiforme (Wollny) Kuck.

Epilithic and on *Balanus* in the upper sublittoral from September to April, sporangia from October to April, Stations 1, 2; also, sparingly present on supralittoral wood pilings in January, the plants bearing sporangia, Station 3. (See Wilce, *et al.* 1970b).

Myrionema aecidioides (Rosenv.) Sauv.

Endophytic in the worn tips of *Laminaria saccharina*,

plurilocular organs from July through December, unilocular organs not encountered. Stations 1, 2.

DICTYOSIPHONALES

Petalonia fascia (O. F. Muell.) Kuntze

A dominant member of the winter algal vegetation, *Petalonia fascia* was first apparent from September to late October in the sublittoral and lower littoral at Stations 1-4; *P. fascia* disappeared from all localities by mid-June.

Only plurilocular organs were seen on the Ipswich plants of *Petalonia fascia*; fusion of motile cells released from these organs was not observed. When cultured, motile cells from plurilocular organs gave rise to filamentous plants which remained vegetative, in contrast to those described by Dangeard (1964) where unilocular sporangia developed on microthalli of *P. zosterifolia.*

Wynne's (1969) thorough study of *Petalonia fascia* from the California and Washington coasts demonstrates that blades of this species with plurilocular organs produce swarmers which grow into microscopic crusts. In turn, the crusts may bear unilocular sporangia, new erect blades, or both, depending upon culture conditions. Wynne did not observe fusion between motile cells from either blades or crusts. He suggests an asexual alternation in *P. fascia* which is facultative, with cool temperatures and short days favoring development of the blade stage, while warmer temperatures and long days induce crust formation.

On the basis of our observations, the most common life history pattern of *Petalonia fascia* in the Ipswich marsh appears to omit the crustose stage. A strict seasonality of thallus development occurs, the plants of which mature to form plurilocular organs. Swarmers from plurilocular organs develop into microthalli which ultimately give rise to erect blades by repeated vegetative divisions. Our field observations corroborate those of Wynne's from culture suggesting a light-temperature relationship for the initiation of new blades. While it is possible that the smallest crustose stages of *P. fascia* were overlooked at Ipswich, we prefer to believe the plants we studied did not possess the alternate

pattern of development involving the crusts and connecting filaments described by Wynne in California plants (1969), and Wilce in plants from West Greenland (1970a).

Scytosiphon lomentaria (Lyngb.) Link

A conspicuous winter dominant in the sublittoral and littoral, *Scytosiphon lomentaria* appeared at Ipswich in early September and persisted until the first week in May. This species was abundant at Stations 1, 2, and sparingly present at Station 3.

At the Ipswich marsh, *Scytosiphon* exists as two morphologically and spatially distinct populations, overlapping in their seasonal occurrence; we have referred to these as population "a" and population "b". Population "a" consists of plants to 35 cm tall, attached to stones and shells in the upper sublittoral and lower littoral. The plants had plurilocular reproductive structures from September to early May. Population "b" is composed of dwarf plants having a maximum length of 7 cm, no constrictions in the cylindrical thalli, and attached to plant debris and mud along the seaward edge of the marsh at Stations 1, 2. Plurilocular organs were formed in March and persisted through early May, soon after which this population was no longer evident on the marsh.

The problems encountered in attempting to interpret the life history of *Scytosiphon lomentaria* are similar to those already discussed in *Petalonia fascia,* i.e., the lack of sexuality, the apparent loss of the gametophyte phase, and the repeated formation of tubular, erect plants developing from microthalli. Culture conditions used to grow isolates of *Scytosiphon* were not varied, but under the uniform conditions previously described the following developments occurred. Motile cells from both "a" and "b" populations gave rise to microthalli; microthalli formed pluricular sporangia from which zoospores repeated the filamentous generation. Eventually, microthalli produced erect *Scytosiphon* plants through vegetative development. Crusts were not seen in natural collections that could be related to the erect thalli of either the dwarf or the larger *Scytosiphon* plants, nor were crusts observed in culture material of either popula-

tion. Wynne (1969) demonstrated however, that, as in *P. fascia*, the crust stage of *Scytosiphon* can be induced environmentally.

Dictyosiphon chordaria Aresch.

Collected once, June, 1963, epilithic in the sublittoral. Station 2.

LAMINARIALES

Chorda filum (L.) Stackh.

This species is a strict summer annual at the Ipswich marsh, occurring on rocks and shells in the sublittoral from June through August, and forming sporangia during July and August. Stations 1-2.

Laminaria saccharina (L.) Lamour.

The only species of *Laminaria* in the Ipswich marsh, *L. saccharina*, encompasses two anatomical varieties with respect to the occurrence of mucilage ducts in the stipes and blades of these plants. These varieties, formerly considered as *L. saccharina* and *L. agardhii* (Wilce, 1965), exist throughout the year at Stations 1-2 attached to rock, shell and wooden pilings. Sori with mature sporangia occurred in these populations from late October through March.

FUCALES

Fucus distichus L. emend, Powell ssp. *evanescens* (C. Ag.) Powell

This species, common but not abundant, occurs at Ipswich only at the littoral-sublittoral interface attached to the occasional large rock at Stations 1-2. Plants of this species were reproductive from April to June. As the uppermost vertical extension of *Fucus distichus* coincides with extreme low later level, the occurrence of these plants offers a fairly accurate reference to aid in determining the approximate level of the tide.

Fucus vesiculosus L.

Epilithic in the sublittoral and littoral, reproductive essentially throughout the year, this species constitutes the greater portion of the macroscopic algal vegetation along the Castle Neck River, Stations 1, 2; a few plants occurred at Station 3.

Ascophyllum nodosum (L.) Le Jol.

Plants of *Ascophyllum* occurred in the same habitats and at the same stations as did *Fucus vesiculosus*. This species, however, never developed the luxuriancy or the abundance seen in populations of *F. vesiculosus*. *A. nodosum* could be found reproductive from late November through March.

MARSH FUCOIDS

The marsh fucoids, *Fucus vesiculosus* var. *spiralis* Farl. and *Ascophyllum nodosum*, *f. scorpoides* (Horn.) Reinke constitute a prominent feature of the algal vegetation on the marsh at only one small area of the littoral zone along the Castle Neck River (Station 2). Marsh fucoids undoubtedly occur elsewhere in the broad expanses of the Ipswich Marsh, but they were not otherwise seen in that portion of the marsh represented by our transects.

Plants of both species referred to above are unattached at Station 2 and cover most of the marsh surface in the Spartinetum alternifloretum. These free-living forms or "ecads" of the typical *Fucus vesiculosus* and *Ascophyllum nodosum* are consistently smaller than their attached counterparts, are usually spirally twisted with more numerous branching, and only rarely become reproductive.

Owing to their frequent dense populations in salt marshes, ecads of *Fucus* and *Ascophyllum* represent adaptable tools of research for the phycologist interested in vegetative and reproductive development, and the factors that control these phenomena. Some attempts were made to determine the potential of different ecads to revert to the species habit, but with little success. A more extensive discussion of these plants will be presented in a paper dealing with the ecology of the Ipswich marsh algae.

RHODOPHYTA

For the systematics of the red algae we have followed essentially the treatment used by Taylor (1957); for *Trailliella*, *Antithamnion*, and species of *Ceramium* and *Polysiphonia*, we have relied on Rosenvinge (1909-1931).

BANGIALES

Erythrotrichea carnea (Dillw.) J. Ag.
Epiphytic on *Ceramium*, *Chondrus*, and *Polysiphonia*, July to October. Stations 1, 2.

Goniotrichum alsidii (Zanard.) Howe
Epiphytic on *Ceramium*, *Polysiphonia*, and *Ascophyllum*, July to October, Stations 1-3.

Porphyra umbilicalis (L.) J. Ag.
Epilithic at low tide level, located only in June, 1963. Stations 1, 2.

CRYPTONEMIALES

Dumontia incrassata (O. F. Muell.) Lamour.
Common on rocks in the sublittoral zone, February through May, tetraspores in May. Stations 1, 2.

Hildenbrandia prototypus Nardo
Epilithic at low tide level through the year, tetraspores from July to October. Stations 1, 2.

Gloiosiphonia capillaris (Huds.) Carm. ex Benk.
Sublittoral zone, Castle Neck River, May, 1965, with cystocarps. Station 2.

Euthora cristata (C. Ag.) J. Ag.
Washed ashore during autumn and spring, tetraspores in March. Station 2.

GIGARTINALES

Agardhiella tenera (J. Ag.) Schmitz
Located only during June and July, 1963, the plants vegetative and epilithic in the sublittoral zone. Stations 1, 2.

Gracilaria verrucosa (Huds.) Papenf.
Seen only in June, 1963 and February and October, 1964, epilithic in the sublittoral zone, cystocarps in October. Station 2.

G. foliifera (Forssk.) Børg.
Epilithic in the sublittoral zone through the year, cystocarps in February and July. Station 2.

Chondrus crispus Stackh.
On sublittoral rocks through the year, carpospores from summer to December, tetraspores from December through March. Stations 1-4.

RHODYMENIALES

Halosaccion ramentaceum (L.) J. Ag.

Abundant in the sublittoral zone from June to August, 1963 only, tetraspores always present. Station 2.

CERAMIALES

Trailliella intricata (J. Ag.) Batt.

The Ipswich plants agree with the original description of this species by Batters (1896) and with subsequent descriptions by Rosenvinge (1909-1931) and Taylor (1957). Tetrasporophytes occurred in October, 1964. These collections add to the few reports (Lewis & Taylor, 1928; Taylor, 1941; Chen, et. al., 1969) of *Trailliella* tetrasporangia from northeastern North America. Fully developed sporangia were observed, measuring 68-74 μ wide and 49-53 μ long, and occurring in a linear series.

The occurrence of *Trailliella intricata* was never large and in the Ipswich marsh it was seen only at Station 1. The small sample of tetrasporangia found in October, 1964 is not sufficient for generalizations as to their yearly occurrence in the marsh. It is noteworthy, however, that the date of our collections of tetrasporangia bearing plants coincides with a recorded peak of abundance of these organs from plants in the Northumberland Strait, and the Atlantic Coast of Nova Scotia, Canada (Chen, et. al., 1969).

Antithamnion cruciatum (C. Ag.) Naeg.

Entangled among *Agardhiella*, June, 1963. Station 1.

Ceramium diaphanum (Lightf.) Roth.

Epilithic in the sublittoral zone, June to September, tetraspores in June and July. Station 3.

C. fastigiatum (Roth.) Harv.

Male, female, tetrasporophytes during the year, epilithic in the sublittoral zone, Station 3. Only tetrasporic plants occurred during September and October at Stations 1, 2.

C. rubrum (Huds.) C. Ag.

Epilithic, also epiphytic on *Gracilaria foliifera*, June to November with tetraspores, cystocarpic plants in July and November. Stations 1, 2.

C. rubriforme Kylin
Epilithic in the sublittoral with cystocarps, July to September. Station 2.

Ptilota serrata Kuetz.
Washed ashore in January and March, 1963, tetraspores in March. Station 2.

Phycodrys rubens (L.) Batters
Washed ashore October to March, cystocarps in January, tetraspores in November, January, and March. Station 2.

Polysiphonia flexicaulis (Harv.) Collins
Seen only in June, 1963, epilithic in the sublittoral. Station 3.

P. urceolata (Lightf. ex Dillw.) Grev.
On small stones, July through September, the plants small (to 6 cm), remaining vegetative. Substation 5a.

P. denudata (Dillw.) Grev. ex Harv. in Hook.
Epilithic in the sublittoral zone from July through December, cystocarps from June to October, tetrasporophytes in August. Stations 2, 3.

P. nigra (Huds.) Batt.
Epilithic in the sublittoral, March to October, with male plants in June, female and tetrasporophytes from July to October. Stations 1, 2.

P. lanosa (L.) Tandy
Epiphytic on *Ascophyllum nodosum*, cystocarps in September, Station 1.

CHRYSOPHYTA

With the possible exception of some species of *Vaucheria*, most recently studied in our area by Blum & Conover (1953), Blum & Wilce (1958), Blum, 1960 and Webber (1968), the salt marsh representative of the classes Xanthophyceae, Dinophyceae, Chrysophyceae and Haptophyceae in North America are poorly understood. We wish to emphasize that most members of these taxa are inconspicuous elements of the cold season salt marsh vegetation, and they represent (especially species of benthic Chrysophyceae and Haptophyceae) a little known area of study for the laboratory or field oriented phycologist.

Data as to the occurrence, seasonal and reproductive periodicities, and life history details of salt marsh members of the above classes are wanting for most. By far the largest number of species have only their occurrence listed for a single or several locations in North America. Experimental research efforts with representatives of these taxa have been initiated recently (e.g., Park, 1961; Boney & Burrows, 1966; Boney 1967). However, many marine species either new to science or previously unknown in North America undoubtedly remain to be described; virtually all of the biology of these species lies in the unknown.

The main references used for the Xanthophyceae (Vaucheriales) were Blum and Conover (1953) and Taylor (1957). Systematic treatments of the remaining classes follows Parke (in Parke and Dixon, 1964).

XANTHOPHYCEAE (Vaucheriales[3])

Vaucheria compacta (Collins) Collins var. *koksoakensis* Blum & Wilce

Conspicuous from May through November carpeting the mud of creek banks, reproductive from July to December. Substation 5a.

V. arcassonensis Dangeard

Forming mat-like expanses in the soil at the bases of *Spartina patens*, reproductive plants located in May, vegetative material apparent from June through August. Station 2.

V. intermedia Nord.

Located in the mud at seaward edges of the marsh, and mixed with *Vaucheria arcassonensis*, the plants reproductive from September through the winter to March, then vegetative and most abundantly so in June and July. Stations 1, 2.

DINOPHYCEAE (Phytodiniales)

Urococcus foslieanus Hansgr.

With *Ruttnera*, this species is an important constituent of the winter microvegetation. *Urococcus* was first lo-

[3]See Webber, 1968.

cated in quantity in *Spartina* debris, where a few isolated cells persisted through the summer. Daughter cell formation was observed in September, 1962 and in January, 1964, but release of these cells was not seen, even after prolonged observation.

CHRYSOPHYCEAE (Ochromonadales)
Ruttnera maritima (Anand) Parke

Plants unicellular, aggregated, with a thick gelatinous matrix, each cell with a parietal chromatophore, numerous oil droplets, and upon several occasions a pyrenoid was observed in each cell.

This species was first located in early November from soil beneath the *Spartina* grasses and from old culms of these plants. At Ipswich, *Ruttnera* was most abundant from January through March, with the populations persisting to early June. The quantities of oil droplets increased and the chromatophore became more diffuse as June approached. Formation and discharge of motile cells was seen from field collections of February, 1964; each cell produced 8 daughter cells which, upon release, showed no evidence of fusion. Under culture conditions of 14°C and 100 f.c. of light, these swarmers grew into small branched filaments floating at the surface of the culture solution. Further attempts to study the continued development of these filaments was unsuccessful.

Anand's (1937a, b) *Ruttnera* species were distinguished by the presence (= *Gloeochrysis maritima* Anand) or absence (= *Gloeochrysis littoralis* Anand) of a pyrenoid. Pyrenoid occurrence in *Ruttnera* cells at Ipswich seems to be variable as observed with the aid of a light microscope. Further, the degree of stratification of the cells' matrix, a species criterion also used by Anand, seems to be ecologically controlled.

It is our opinion that there is insufficient evidence now that these characteristics are valid species criteria. Until additional cytological and morphological data are available, we consider the Ipswich plants as *Ruttnera* sp., with the closest affinity to *R. maritima*.

HAPTOPHYCEAE (Phaeothamniales)

Material of this family representing a new genus will be treated in more detail in a later publication.

Plants filamentous, branching, the branches entangled, cells 6-7 μ diam. and 12-18 (28 μ long, constricted at the septa, chromatophores parietal and band-shaped, 1-3 per cell, lacking pyrenoids.

Of common occurrence in the leeward face of wood pilings in the marsh sublittoral, especially so from early October through the winter to late May.

Acknowledgments

We offer grateful appreciation to Dr. C. Bliding for his generous help in identifying species of *Enteromorpha*, to Dr. C. van den Hoek for confirmations of *Cladophora* determinations, and to Dr. J. L. Blum for advice concerning the Cyanophyta. The senior author acknowledges support of a portion of this investigation through an N.S.F. Summer Fellowship; also, he is deeply appreciative of the assistance given by his wife, Judith.

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GREENMANIA: A TAXONOMIC SYNONYM OF UNXIA (COMPOSITAE: HELIANTHEAE)

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Greenmania and the type species, *G. boladorensis,* were described in 1901 by Georg Hieronymus from material collected by P. Sonntag (*51*) "in monte Bolador" during August of 1881 in Colombia, South America. In 1907 Hieronymus described a second new species in the genus, *G. ulei,* this time from a specimen collected by E. Ule (*5146*) on 29 July 1900 "an feuchten Stellen bei Manaes" in Amazonian Brazil. Examination of the fragments and photographs of the type specimens of these two species in the U. S. National Herbarium has shown that *Greenmania* is congeneric with *Unxia* L.f., a genus recently re-established in the subtribe Melampodiinae and also found throughout the northern regions of South America (Stuessy, 1970). S. F. Blake many years ago perceived the congeneric relationship of these two taxa as evidenced by his handwritten note placed inside the packet containing fragments of the type of *G. ulei,* in which he stated that the species is "a genuine congener of *M*[*elampodium*] *camphoratum*" [=*Unxia camphorata*].

Greenmania thus becomes a taxonomic synonym of *Unxia* (validly published in 1781), and *G. boladorensis* and *G.*

[1]I am indebted to the Ohio State University College of Biological Sciences for financial support during this study (Research Grant 3808).

ulei are included in the synonymy of *Unxia camphorata* L.f. Although the types of the two species of *Greenmania* differ in some quantitative aspects such as pubescence, they both fall within the limits of variation observed for *Unxia camphorata* (Stuessy, 1970).

It is not unexpected that Hieronymus placed *Greenmania* in the subtribe Milleriinae (so indicated in the protologue) instead of in the subtribe Melampodiinae. He accurately recognized the presence of few sterile disc florets which has been considered an important feature of the Milleriinae by Bentham and Hooker (1873) and Hoffmann (1890). *Unxia*, however, is most similar in total morphology to *Polymnia* Cav. in the Melampodiinae even though *U. camphorata* does not possess the large numbers of disc florets characteristic of that subtribe. It is becoming increasingly clear that the Melampodiinae and Milleriinae are artificial units separated by the characters of number of sterile disc florets and the absence or presence of disc paleae. The needed re-alignment of these subtribes along more natural lines, however, must wait until the genera themselves are more perfectly understood.

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A PUNCTARIA NEW TO NEW ENGLAND WATERS

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Several additions to the New England marine flora have of recent years been made by divers, these generally being forms growing rather below the zone where storm waves tear the plants loose and drift them ashore, and possibly are native, possibly introduced. Other additions more certainly represent immigrants from abroad, since they often were first recognized in areas such as that about Woods Hole, Mass., where the shallow water flora has been under close observation for many years. Careful search has shown that these species were not represented in earlier collections, even under misidentifications. When recognized they have generally been found quickly to become frequent or even very common. One can cite *Asparagopsis* and *Trailiella* (now recognized as stages of one species) as being well established examples (Lewis and Taylor 1928, pp. 196, 197), while *Codium* is a new and most aggressive interloper (Taylor 1962, p. 489).

Additions to the records of minute species are to be expected, and adjustments in nomenclature made where some of these are found to be stages in the life histories of larger species, but few native novelties of large species are likely to turn up from shallow water. The variety of *Punctaria* (Phaeophyceae: Punctariales; Punctariaceae) here described seems to be an exceptional one of these.

Punctaria plantaginea (Roth) Grev., n. var. **rugosa**:— Plants very irregular in shape, reaching 1 dm. in width, 3 dm. in length, when mature loose on the bottom. The central portion of the blade is flat or a little undulate, the marginal portions highly crisped or convolute in an irregular band 1-3 cm. in width. The thickness of the blade varies from 4-7 cells and 105-180 μ, in the central portion usually being 6 cells thick. MASSACHUSETTS: Barnstable

[1]I am indebted for the latin diagnosis to Dr. Hannah Croasdale of Dartmouth College. This report covers a small part of a more general study conducted with the aid of Grant GB-3186 from the National Science Foundation, which help is most highly appreciated.

County, Town of Gosnold, Cuttyhunk Island, from Gosnold Pond at the east end of the island in about 3 dm. depth of water. Collected by *W. R. Taylor*, 8 Aug. 1963. Type material in the herbaria of the University of Michigan and the author. Figure 1, × 1.2.

Punctaria plantaginea (Roth) Grev., n. var. **rugosa**: — Plantae maturae non affixae, forma irregulares, in centro laminarum fere planae, circum margines late intricateque crispatae convolutaeve. Plantae typicae in lacuna Gosnoldii in insula Cuttyhunk dicta, in urbe Gosnoldii, in comitato Barnstable dicto, Massachusetts, U. S. A., a *W. R. Taylor*, 8 Aug. 1963 lectae, in herbariis Taylorii et Universitatis Michiganensis depositae. Fig. 1, × 1.25.

These plants differ so widely from typical material that only when there is close familiarity with both can the relationship be quickly recognized in the field. The typical form of the species appears as flat or slightly undulate

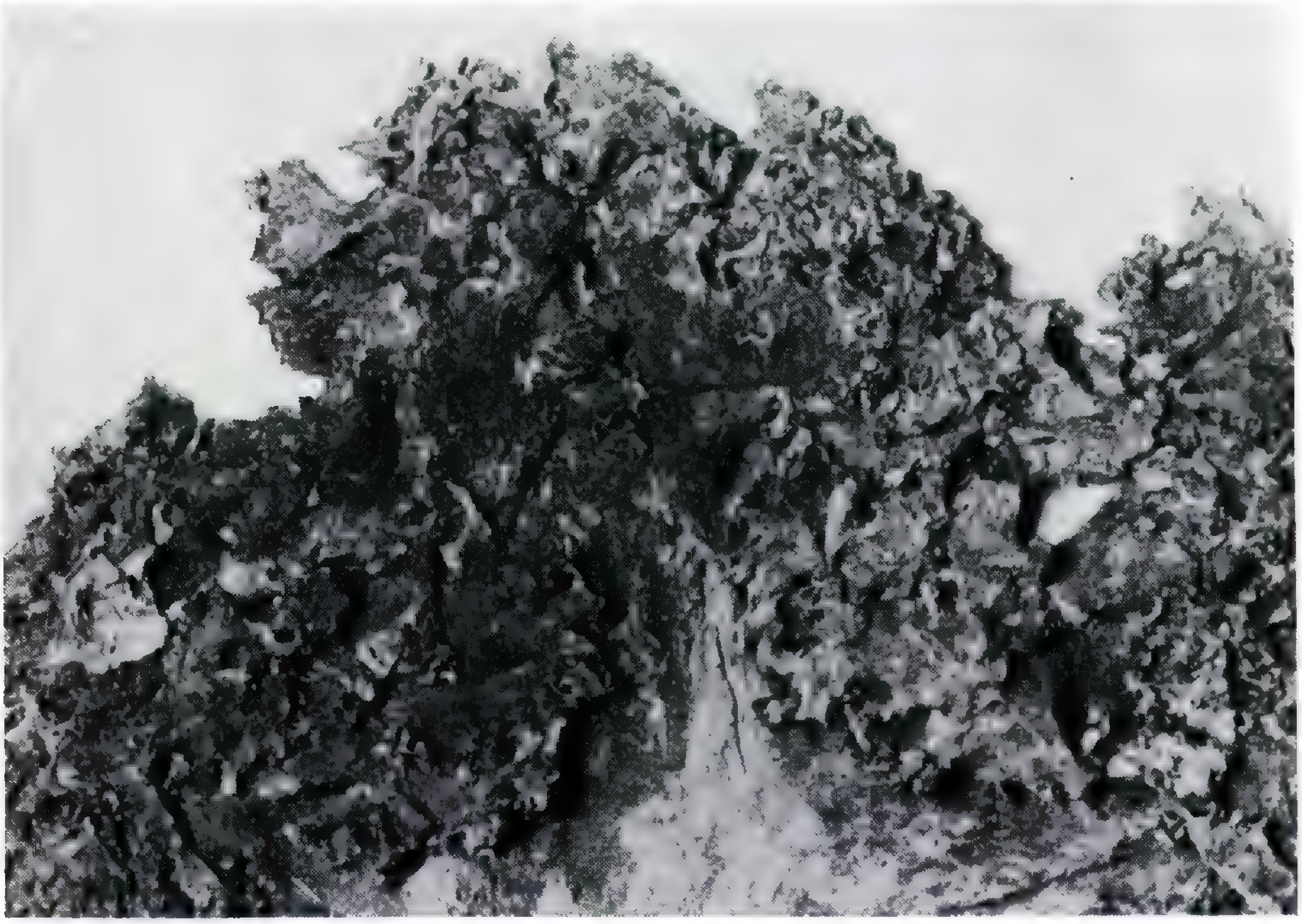

Figure 1. *Punctaria plantaginea* n. var. *rugosa* — A portion of the margin of a thallus from a pressed herbarium specimen, the elaborateness of the convolutions therefore not shown to the best advantage. The margin of the plane center of the thallus shows at the lower center of the photograph. × 1.2

blades basally attached, usually 2-6 dm. long. These varietal plants are so irregular in outline that it is generally not possible to distinguish length from breadth. They are more fragile than typical individuals, but the thallus color, thickness and texture otherwise conform. It was not practicable at the time the original collection was made to trace the growth stages of these plants, so it is not known at what time they become detached from their presumably firm first substrate. As found they were loose on the somewhat muddy bottom of this tidal pond, in an area probably somewhat brackish and certainly not disturbed by more than the slightest wind ripples, being entirely sheltered from sea waves by the barrier beach.

There is some similarity between this plant and the thinner Alaskan *P. chartacea* Setch. and Gardn. (1924, p. 4), but the marginal fimbriate character of the eastern plant is less spectacular than is the complex wrinkling or, in the sense of the term as applied to the human brain, convolution of the outer areas of the blades. Kützing (1843, p. 299; 1856, p. 18) recognized *Phycolapathum crispatum* from the Adriatic as having a fimbriate margin, but his illustration does not suggest the characters of the plant here described. So far as I am aware Kützing's species has not been transferred to *Punctaria*, and in any case it is doubtful if the New England plant qualifies for species rank.

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AN INTERESTING ASSOCIATION OF RARE AQUATIC PLANTS FROM NEW HAMPSHIRE

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New stations for any plant are of special interest to the botanist, particularly when several rarities are found within a given habitat, and more particularly when the habitat is well known yet by-passed by literally thousands of travellers annually. The three authors were returning from a field trip to Maine in the summer of 1970 and stopped at the large pond-like area formed by the overflow of the Taylor River on the west side of the New Hampshire Turnpike at the Hampton-Hampton Falls line in Rockingham County, New Hampshire. As visitors to this area will readily recall, approximately one mile south of the Hampton Tollgate on the south-bound side there is a roadside rest area used by travel-weary drivers for some years. All collections were made from within several hundred meters of this place.

Along this portion of the turnpike the water's edge parallels the roadway at a distance of roughly thirty meters. At the rest area the edge of the water turns abruptly westward at virtually right angles to the road. We were able to collect from both the east and south sides of this corner of the pond both by hand and by using a weighted thrownet to recover specimens where deep mud made wading impractical. Algae and small aquatics were preserved in FAA, and larger vascular plants were pressed on the spot. Representative specimens are being placed in local herbaria, the algae at Boston State College and Boston University; the vascular aquatics at Boston State College and the University of New Hampshire.

Examination of the water along the west edge of the turnpike revealed the presence of an extensive mat of *Hydrodictyon reticulatus* (L.) Lagerheim. The mat ranged from the water's edge outward for three to five meters and extended from the pond corner northward for more than fifty meters. We collected the species from both Hampton and Hampton Falls in as much as this Chlorophycean alga

has not been previously reported from New Hampshire. Upon closer examination of the material in the laboratory we were able to identify another new record for the state in *Lyngbya aestuarii* (Mert.) Liebmann, a Cyanophycean species entangled within the netlike structure of the *Hydrodictyon.*

Hydrodictyon has been reported from Connecticut by Conn & Webster (1908), by Hylander (1928); from Massachusetts by Croasdale (1935) and Auyang (1962); and from Vermont by Flint (1916) and by Joyce (1936). *Lyngbya aestuarii* has been reported from Connecticut by Holden (in Collins, 1905), Setchell (in the Phycotheca Borealis-Americana, No. 6), and by Hylander (1928). This species has also been reported extensively from southeastern Massachusetts.

This southeast corner of the pond appeared to collect considerable amounts of surface material drifted or pushed by wind action. At the time we visited the site much of the surface near the shore was covered by a floating blanket of both living plants and debris. *Lemna minor* L. was the most prevalent species, but close examination of the drift revealed the presence of considerable quantities of *Wolffia columbiana* Karst. During the preparation of this paper for publication the authors were advised by Albion R. Hodgdon of the University of New Hampshire that this apparently was only the second collection of this species of *Wolffia* within New Hampshire. The previous report, which we confirmed with the author, was by William D. Countryman of Norwich University, and detailed the finding of both *W. columbiana* Karst and *W. punctata* Grisebach in a small pond alongside Interstate Highway 93 near Manchester, in Hillsborough County. That both collections should be reported from sites close to major highways, both presumably frequented by area botanists, is of interest in itself.

Close examination of the *Lemna,* incidentally, revealed that many of its leaf cells were hosting the tiny Chlorophycean endophyte *Chlorochytrium Lemnae* Cohn, a species of algae previously reported from Rockingham County by

Frank S. Collins (1905). The three genera *Lemna, Wolffia,* and *Chlorochytrium* are hereby reported for both Hampton and Hampton Falls.

Material gathered by using the net produced three species of larger vascular aquatics. Common along both the east and south shores was *Elodea Nuttalli* (Planch.) St. John. In material collected from the water along the south shore we found a few specimens of *Potamogeton perfoliatus* L. var. *bupleuroides* (Fern.) Farw. Also common to the material recovered along both shores was *Potamogeton obtusifolius* Mert. & Koch. From examination of specimens in the Herbarium of the New England Botanical Club and the Herbarium of the University of New Hampshire it would appear that this is the most southeasterly collection for this species in New Hampshire.

Potamogeton obtusifolius has been reported from Coos County by both A. S. Pease (1912) and S. B. Krochmal (1950). Dodge and Woolner collected it in Carroll County (1946); A. S. Pease in Grafton County (1937); Krochmal again in Hillsborough County (1946), and at Deerfield in Rockingham County in 1950. The present collection, from a former estuary, seems to be from habitats that more closely resemble several collections of the species from near the ocean in Essex County, Massachusetts. On the surface it would appear that this species tolerates a rather wide range of salinity, but insufficient data exists with the material available to be able to state this as a valid premise.

In retrospect, the location of this site, so close to a major artery over which the authors have individually and collectively travelled for some years points up the temptation to overlook the ground "under our feet" in favor of those other pastures that appear more verdant. It also seems worthwhile to suggest that a more prolonged and intensive investigation of this area might disclose other unusual species. Albion Hodgdon, in a personal communication to the authors, was of the opinion that this area, being of estuarine origin, still contained considerable quantities of salts both in and on the bottom, and we might add, these

might serve to structure, in combination with the everpresent fresh water, an unusual community.

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VASCULAR PLANTS NEW FOR OKLAHOMA, KANSAS AND NEBRASKA

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As a result of field and herbarium studies recently completed, several previously unreported vascular plants were found for Oklahoma, Kansas and Nebraska. A new form of *Commelina erecta* with white flowers was found in Kansas and a white flowered form of *Aster oblongifolius* was found in Kansas by the author and by H. A. (Steve) Stephens in Nebraska. Special thanks are due to Dr. R. L. McGregor for his help and encouragement during this study.

Commelina erecta L. var. **erecta** f. **alba** Magrath, form. nov. A forma *erecta* differt petalis albis.
TYPE: KANSAS: Chase Co.: 6.3 mi w of Strong City, roadside ditch by creek, semi-wooded area, small colony, 4 October 1969, *Magrath, J. E. & B. L. Taylor* 4990 (Holotype: KANU!). All of the plants in this small colony had white flowers in contrast to f. *erecta* where the upper petals of the flower are blue. A white flowered form (f. *albina* Fern.) has been reported for var. *angustifolia*.

Spiranthes lacera (Raf.) Raf. NEBRASKA: Franklin Co.: 1896, *W. A. Harshberger* 4684 (NEB). Johnson Co.: 0.6 mi n of Cook on N 50, prairie hay meadow, loam, rare, 26 September 1970, *Magrath* 6342 (KANU). Otoe Co.: 6.5 mi s of Syracuse on N 50, prairie hay meadow, loam, rare, 26 September 1970, *Magrath* 6345 (KANU). Pawnee Co.: 0.6 mi s of Pawnee-Johnson Co. line on N 50, prairie hay meadow, loam, rare, 26 September 1970, *Magrath* 6341 (KANU). The Harshberger specimen had originally been determined as *Ibidium gracile* (Bigel.) House and is so listed by Winter (1936). There is however some question as to whether or not this specimen was actually collected in Franklin Co. At some time in the past a question mark has been penciled on the label with reference to the location.

Spiranthes lucida (H. H. Eaton) Ames NEBRASKA: Cass Co.: South Bend, moist land, 20 July 1896, *G. G. H.*, s.n.

(MO). This previously unreported station represents an extension of the range of this species to the north and west in the central plains region. In Kansas this species is known from a single specimen collected in Cloud Co. by S. V. Fraser (KSC) in 1930, and it has not been found again in the state. In Missouri (Steyermark, 1963) it is restricted to the southeastern Ozark area in St. Francois, Reynolds, Dent, Shannon, Oregon, Texas and Howell counties. Correll (1950) considered both the Kansas and Missouri stations as representing disjunct areas.

Spiranthes vernalis Engelm. & Gray NEBRASKA: Cass Co.: 1 1/2 mi w of Cedar Creek, collected at the edge of a sandy area along the Platt River, 17 August 1933, *Morrison*, s.n. (NEB). Hall Co.: 0.5 mi e (on US 30), 6 s & 0.7 w of Wood River, prairie hay meadow on s side of Platte River, sandy-loam, rare, 23 August 1970, *Magrath* 6059 (KANU). Johnson Co.: 0.3 mi s of the Johnson-Otoe Co. line on N 50, prairie hay meadow, loam, growing near *Equisetum*, uncommon, 3 August 1970, *Magrath* 5723 (KANU). Nemaha Co.: 5.5 mi s of Auburn on US 75, growing in uncut native prairie area in a cemetery on e side of hwy., rare, loam, 3 August 1970, *Magrath* 5716 (KANU). Otoe Co.: Nebraska City, 14 August 1900, *G. G. H.*, s.n. (MO). Pawnee Co.: 0.6 mi s of Pawnee-Johnson Co. line on N 50, prairie hay meadow, loam, rare, 3 August 1970, *Magrath* 5715 (KANU). The NEB specimen was incorrectly identified as *S. cernua*, and the MO specimen as *S. gracilis*. Correll (1950) reports this species from Otoe Co., however Winter (1936) does not list it for the state.

Corallorhiza odontorhiza (Willd.) Nutt. NEBRASKA: Richardson Co.: Missouri River Bluffs, 4.4 mi s & e of Rulo. loess soil, oak woods, rare, 26 September 1970, *Magrath* 6327 (KANU). This is an extension west from Iowa (Correll, 1950) and north from Kansas (Barker, 1967).

Brasenia schreberi Gmel. KANSAS: Johnson Co.: 1.5 mi s of Olathe (s of K 7), South Olathe City Lake, found growing in lake, rooted in mud, in fruit, rare, 18 October

1970, *Magrath* 6640 (KANU). Muenscher (1944) indicated the presence of this plant in Kansas. However there are no known specimens in any of the regional herbaria to substantiate this report.

Cabomba caroliniana Gray KANSAS: Johnson Co.: 1.5 mi s of Olathe (s of K 7), South Olathe City Lake, found floating free in lake, apparently rare, in flower, 18 October 1970, *Magrath* 6639 (KANU). This is an extension west from Missouri (Steyermark, 1963) and north from Oklahoma (Waterfall, 1966). Since this plant is frequently used in aquaria, it is possible that it may have been introduced into the lake sometime in the past.

Actaea alba (L.) Mill. NEBRASKA: Richardson Co.: Missouri River Bluffs, 4.4 mi s & e of Rulo, loess soil, oak woods in shaded area, n-facing slope, one plant seen, 26 September 1970, *Magrath* 6326 (KANU). In Kansas it is known only from Doniphan Co.: *Horr* 4267 (KANU). In Missouri (Steyermark, 1963) it occurs in the Ozarks, northern and northwestern parts of the state.

Ribes missouriense Nutt. OKLAHOMA: Ottawa Co.: 1 mi s & 0.8 w of the Kansas-Oklahoma St. line on a county rd. (or 6 mi s & 0.8 w of Galena), river bottom woods, shrub 2-3 ft, one bush observed, apparently rare, 2 May 1970, *Magrath* 5167 (KANU).

Polygala senega L. var. **latifolia** T. & G. KANSAS: Cherokee Co.: 0.8 mi e & 3.6 s of the Jct. of K 26 & US 66 in Galena, oak-hickory timber, gravelly-loam, one plant with two stems observed, 4 September 1969, *Magrath* 4828A (KANU). This represents an extension from the Missouri (Steyermark, 1963) and Oklahoma (Waterfall, 1966) Ozarks into southeastern Kansas.

Monotropa hypopithys L. NEBRASKA: Box Butte Co.: near Alliance, 1909, *Churchill* (NEB). Richardson Co.: 3 mi s & e of Rulo, wooded hillside near Missouri River, single stem was observed, 11 October 1969, *Magrath & Mennell* 5043 (KANU). The Churchill specimen had been identified as a *Corallorhiza*. The locations of these two

specimens creates an interesting distribution pattern for the state, in that the Magrath & Mennell specimen is from the extreme southeast corner and the Churchill specimen is from the northwestern corner. In Kansas the plant is known from Cherokee Co.: *Magrath* 4962 (KANU) and Douglas Co.: *McGregor* 5667 (KANU).

Bacopa acuminata (Walt.) Robins KANSAS: Cherokee Co.: 2.5 mi s of Galena, open rocky oak-hickory woods near Shoal Creek, scattered, 25 August 1969, *Magrath* 4599 (KANU). In Missouri (Steyermark, 1963) the plant is known from Newton, Jasper, Dunklin and Mississippi counties.

Hedyotis longifolia (Gaertn.) Hook. KANSAS: Cherokee Co.: 3.6 mi s & 0.9 e of Galena, Ozark oak-hickory woods, rocky soil, growing at edge of old road through woods, rocky soil, 28 September 1969, *Magrath* 4965A (KANU).

Aster oblongifolius Nutt. var. **oblongifolius** f. **albaligulatus** Magrath, form. nov. A forma *oblongifolius* differt ligulis albis.

TYPE: KANSAS: Smith Co.: 2.8 mi n of Harlan on US 281, rocky outcrop on road cut at edge of small native prairie on abandoned highway right-of-way, one small colony observed, 5 October 1969, *Magrath, J. E. & B. L. Taylor* 5021 (Holotype: KANU!). NEBRASKA: Sarpy Co.: 7 mi s, 2 e Gretna, north bluff of Platte River, rocky, sandy, clay soil, rare, 30 September 1969, *Stephens* 37012 (KANU). The Smith Co., Kansas colony was revisited again on 29 September 1970 and a second collection (*Magrath* 6497A) was made at that time. The specimens were pure white when collected and remained this color after having been dried.

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DEPARTMENT OF BOTANY
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REDISCOVERY OF ECHINACEA TENNESSEENSIS (BEADLE) SMALL: Although *E. chinacea tennesseensis* is listed by Small (1933) as occurring on "gravelly hillsides, Interior and Ozark Plateaus, Tenn. and Ark.", the only specimens cited by McGregor (1968) were from Rutherford County, Tennessee. In fact, McGregor (1968) had considered the species probably extinct until a population was reported in an open cedar glade on Mt. View Road, Davidson County, Tennessee (Baskin, Quarterman and Caudle, 1968). Since that time, another population has been discovered (August, 1970) in cedar glades in and near Cedars of Lebanon State Forest, in Wilson County, Tennessee. These are the only presently known populations of a species which, according to McGregor (1968), may now be considered endemic to cedar glades of Tennessee. The population on Mt. View Road is being encroached upon by housing and by increasing road shoulder maintenance, but the population on state land in Wilson County is not presently threatened. This population is large enough to insure continued existence of the species, at least for a time. A pop-

ulation on the area believed to be the type locality has been destroyed by recent construction of a trailer park.

Taxonomists interested in study material are encouraged to rely on collections already in existence, in the interest of preservation of the species. Specimens are known to be located in the herbaria of Mississippi State University, University of Kansas, University of Tennessee, and Vanderbilt, in addition to those cited by McGregor (1968).

An ecological study of the species including consideration of its ecological amplitude and reproductive potential as related to its endemism was recently initiated by the junior author.

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FUNGI ISOLATED FROM THE FRUITS AND SEEDS OF SOME NORTHERN HARDWOOD TREES*

JAMES H. FRIDRICH, AVERY E. RICH, AND ALEX L. SHIGO

Seed-borne fungi have been reported on or in the fruits and seeds of many horticultural and agronomic plants. There are relatively few reports, however, of fungi borne on the fruits and seeds of forest trees, especially of deciduous trees in North America. Ames (1952) isolated *Gleosporium ulmicolum* Miles from the fruits of rock elm (*Ulmus thomasi* Sarg.) and variegated English elm (*U. procera* cv. *argenteovariegata* West.). Shigo and Yelenosky (1963) isolated *Coniothyrium* sp., *Penicillium* spp., *Aspergillus* spp., *Alternaria* sp. and *Trichothecium roseum* Link ex Fr. from yellow birch (*Betula alleghaniensis Britt.*) seeds. In view of these limited reports it was decided to determine further the presence of seed-borne fungi in the fruits and seeds of some northern hardwood trees.

Fruits and seeds were collected from 4 yellow birch, 3 paper birch (*Betula papyrifera* Marsh.), 2 silver maple (*Acer saccharinum* L.), 2 red maple (*A. rubrum* L.), 3 sugar maple (*A. saccharum* Marsh.), and 3 white ash (*Fraxinus americana* L.) from New Hampshire and Massachusetts. The 17 collections were made during the fall of 1967 and the spring and summer of 1968 when the fruits and seeds were mature but still on the tree. All the collections except those from silver maple and red maple were air dried before isolations were made.

Fungi grew from most of the fruits and seeds. The percentage ranged from 93% of 1 yellow birch collection, to 13% of 1 paper birch collection. Several different fungi were isolated occasionally from the same fruit or seed. Fungi representing 30 genera were isolated (Table 1). *Alternaria tenuis* auct. sensu Wiltsh. and species of *Penicil-*

*Published with the approval of the Director of the New Hampshire Agricultural Experiment Station as Scientific Contribution No. 507.

lium and *Aspergillus* were isolated from all collections except for 1 from paper birch. *Coniothyrium* sp. was present in 15 collections; *Botrytis cinerea* Pers. ex Fr. in 12; and *Epicoccum purpurascens* Ehr., *Phomopsis* sp., and *Physalospora obtusa* (Schw.) Cke. in 9. *Fusarium* spp. was present in only 6 of the collections but in 1 yellow birch collection it was isolated from 93% of the 200 seeds. *Gleosporium* sp. was present in only the 2 silver maple collections where it was isolated from more than 20% of the fruits. Some of the remaining species of fungi were present in as many as one-half or more of the 17 collections but were rarely isolated from more than 5% of the 200 fruits or seeds from each collection. Several fungi did not sporulate on malt-yeast agar and were not identified.

A variety of fungi are able to invade the fruits and seeds of some northern hardwood tree species. The list presented here would undoubtedly be expanded if a greater number of trees were sampled. Most of the fungi are probably saprophytes on or in the dead tissues of the fruit or seedcoat. Some may be pathogens. Conditions favorable for the invasion of these fungi might reduce germination or weaken seedlings, making them vulnerable to environmental stresses.

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TABLE I

Fungi isolated from fruits and seeds of 6 species of northern hardwood trees.

Fungus isolated	Tree Species Yellow birch 4 lots	Paper birch 3 lots	Silver maple 2 lots	Red maple 2 lots	Sugar maple 3 lots	White ash 3 lots
Alternaria tenuis auct. sensu. Wiltsh.	+	+	+	+	+	+
Aspergillus spp.	+	+	+	+	+	+
Botrytis cinerea Pers. ex. Fr.	+	+	+	+	+	+
Cephalosporium sp.	0	0	0	0	0	+
Chaetomium funicola Cke.	+	0	0	0	0	+
Chaetomium globosum Kunze ex. Fr.	+	0	+	0	0	+
Chaetophoma sp.	0	0	0	0	+	0
Coniothyrium sp.	+	+	+	+	+	+
Curvularia inaequalis (Shear) Boed.	0	0	+	+	0	0
Cylindrocephalum sp.	0	0	0	0	+	0
Cytospora sp.	0	0	0	0	+	0
Diplodia sp.	0	0	0	+	+	0
Epicoccum purpurascens Ehr.	+	+	+	+	0	+
Fusarium spp.	+	+	+	+	0	+
Fusidium sp.	0	0	0	0	+	0
Geotrichum spp.	0	0	+	+	0	+
Gleosporium sp.	0	0	+	0	0	0
Helminthosporium sp.	+	0	+	0	+	+
Hormodendron sp.	+	+	+	+	+	+
Mucor sp.	0	0	0	0	+	+
Paecilomyces sp.	0	0	0	0	+	0
Penicillium spp.	+	+	+	+	+	+
Phomopsis sp.	+	+	+	0	0	+
Physalospora obtusa (Schw.) Cke.	0	0	+	+	+	+
Pleospora sp.	0	0	0	0	0	+
Rhizopus sp.	+	+	0	0	+	+
Sordaria fimicola (Rob.) Ces. & de Not.	0	0	+	0	0	+
Sporotrichium sp.	0	+	0	0	0	0
Stemphylium consortiale (Thum.) Groves & Skolko	+	0	0	+	0	0
Trichoderma viride Pers. ex Fr.	0	0	+	+	+	+
Verticillium sp.	+	0	0	0	0	0

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JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Conducted and published for the Club, by

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Vol. 73 September, 1971 No. 795

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The New England Botanical Club, Inc.

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LEXINGTON, MASSACHUSETTS

Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 73 September, 1971 No. 795

BIOSYSTEMATIC STUDIES IN THE NORTH AMERICAN GENUS SABATIA (GENTIANACEAE)[1]

JAMES D. PERRY[2]

Sabatia is a herbaceous genus of seventeen species and two varieties which are indigenous to continental North America and the West Indies. They are distributed from central Mexico northward to Nova Scotia and from Oklahoma and Texas eastward to the Atlantic coast.

Although the genus has been subjected to previous revisional treatments (Grisebach, 1839, 1845; Blake, 1915; Wilbur, 1955) and to numerous regional interpretations, very little has been published concerning its cytological and crossing characteristics or breeding systems. Accordingly, this investigation is biosystematically oriented.

HISTORICAL ACCOUNT

The genus *Sabatia* was proposed by Adanson (1763) to commemorate an Italian botanist, Liberato Sabbati. Plants belonging to the genus had been described earler by Gronovius (1739) as species of *Gentiana*. Linnaeus (1753) treated the four species known to him as representatives of the

[1]Based on a dissertation presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany at Duke University. Voucher specimens of species and hybrids are deposited in the herbarium of Duke University.

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genera *Chironia* and *Swertia*. Later he transferred one of the species from *Chironia* to *Chlora*.

Pursh (1814) accepted *Sabatia* and extended it to include the American species placed in *Chironia*. The genus was treated in Grisebach's (1839, 1845) monographs of the Gentianaceae in which were recognized 11 species and one variety. Gray (1878) included 13 species and two varieties in his "Synoptical Flora." Blake (1915) recognized 22 species and one variety which were grouped into subgenera, sections, and subsections. Wilbur (1955) recognized 17 species and two varieties in a systematic hierarchy basically similar to that of Blake.

SYNOPSIS OF TAXA

The following synopsis of *Sabatia* is based upon Wilbur's (1955) treatment which provides the framework for these investigations. Emended descriptions and notes on the ecology, phenology, and distribution of each species are presented. Nomenclatural history, keys, full descriptions, and range maps are given by Wilbur and are not repeated here.

Section I. SABATIA.

Annuals, biennials, or perennials. Branches opposite or alternate. Flowers pedicellate, solitary, or loosely cymose; pentapetalous (annuals and biennials only) or pluripetalous; pink or white. Bracts subtending flowers small and scale-like. Anthers becoming revolutely coiled after pollen release, or recurved. Stigmatic branches usually coiled at maturity. Five subsections, 15 species.

This section contains the type species *S. dodecandra* and must bear the generic name unaltered according to Art. 22, International Code of Botanical Nomenclature (Lanjouw, 1961).

Subsection A. DIFFORMES Wilbur, Rhodora 57: 6. 1955.

Perennials, with thick elongated rhizomes. Branches typically opposite. Flowers pentapetalous (the first and innermost larger, occasionally 6-parted), white. Anthers becoming recurved after pollen release. Stigmatic branches

coiled at maturity. Basal rosette formed during dormancy. Two species.

Sabatia difformis (L.) Druce, Bot. Exch. Club and Soc. Brit. Is. 3: 423. 1914.

Calyx lobes usually more than 4 mm long. Corolla lobes longer than 7 mm. Leaves and upper portion of stem not glaucous. Main stem and branches usually strongly angled.

Sabatia difformis occurs in savannas and pine barrens from central New Jersey southward through peninsular Florida and into western Florida. Individuals have been collected for this study from a river bank in western Florida and from roadside ditches in North Carolina. The species has a weedy habit and may rapidly invade newly cleared areas.

Stems die in the fall, and during winter dormancy one or more small basal rosettes grow from the rhizome. The lowermost leaves are subterranean. With elongation in spring these become cauline leaves. Flowering occurs from late May through late August. Under greenhouse conditions the time from pollination to seed release from the capsule is about three months. Approximately 165 seeds per capsule are produced by artificial selfing. This and subsequent estimates of seed set are based on a minimum of ten self-pollinations.

Sabatia macrophylla Hook., Compan. Bot. Mag. 1: 171. 1836.

Calyx lobes less than 4 mm long. Corolla lobes to 7 mm in length. Leaves and upper portion of stem glaucous. Main stem and branches terete throughout.

Two varieties have been recognized. *Sabatia macrophylla* var. *macrophylla*, having short erect calyx lobes less than or equalling the tube in length, ranges from northwestern Florida and Georgia into Louisiana. *Sabatia macrophylla* var. *recurvans* (Small) Wilbur grows in northeastern Florida and southern Georgia. It has recurved calyx lobes exceeding the tube in length. Both varieties occur in savannas and pine barrens; var. *macrophylla* grows in open flatwoods, swampy meadows, bogs, and on moist grassy slopes. *Sabatia macrophylla* var. *recurvans* grows in seepage areas

which are often wooded, in elevated slash flatwoods and moist sandy savannas, and occasionally in open bogs.

The varieties occupy distinctive geographical ranges which converge in the vicinity of Lake City, Florida. In calyx-lobe length and recurvation, individuals at the western limit of var. *recurvans* do not resemble var. *macrophylla.* In the eastern portion of its range, however, var. *macrophylla* occasionally has a slight recurving of the calyx lobes; the lobes may be longer, though not exceeding the calyx tube in length. Whether this variation in calyx lobe recurvation is sporadic or continuous from west to east has not been determined. No population containing both varieties was located.

Winter dormancy is similar to that of *S. difformis.* The lowermost leaves of the rosette are subterranean. Standing water often covers the plants before elongation in early spring. Flowering occurs from mid-June through July. Under greenhouse conditions the time from pollination to seed release from the dried capsule is about three months. Approximately 90 seeds are produced by artificial selfing.

Subsection B. ANGULARES Blake, Rhodora **17**: 56. 1915.

Biennials, with fibrous roots. Branches typically opposite. Flowers pentapetalous, corollas pink or white. Anthers becoming circinnately recoiled after pollen release. Stigmatic branches tightly coiled at maturity. Basal rosette well-developed and often persisting through anthesis. Three species.

Sabatia angularis (L.) Pursh, Fl. Am. Sept. **1**: 137. 1814.

Corollas pink (rarely white). Calyx lobes usually 1.5 mm or more wide. Lower cauline leaves usually broadly ovate or ovate-lanceolate, often strongly clasping. Lower portion of stem strongly 4-angled, the corners membranous.

Sabatia angularis is the most widespread representative of the genus, ranging from southern New York to northern Florida and westward to Ohio, Illinois, and Texas. Populations occur in fields, prairies, and along margins of woodlands, often near roadsides. Habitats vary from alluvial plains through low, poorly drained pine woods, weedy, clay

roadside banks, and steep slopes of ravines to rich pine-hardwood forests. Large populations grow on granite outcrops in Georgia.

Wilbur (1955) noted that some confusion exists as to whether the species of subsection *Angulares* are annual or biennial; he concluded that they are probably all annuals. Field and greenhouse observations indicate that the species are biennial. Where flowering specimens of *S. angularis* have been seen in the field, nearby rosettes were identical to the persistent rosettes of flowering individuals. Efforts to transplant non-flowering plants to a greenhouse were unsuccessful.

Germination results in a rosette which persists during the first summer and winter; flowering occurs during the second summer. The time of germination in the field was not determined, but it is probably not until spring. The possibility of winter dormancy was investigated. Seeds from selfed pollinations were collected from one plant (*Perry* 1303c, Durham Co., N.C.) and separated into two treatments: half were stored for six months at 35°F; the remainder were stored at room temperature (74°F) for the same amount of time. At the end of this period seeds were sown on filter paper in petri dishes. Those seeds subjected to the cold treatment germinated within nine days and within 20 days all except 12 of the 300 seeds had germinated. Seeds not preconditioned germinated slowly. Two of 300 seeds germinated in 20 days, and germination subsequently was sporadic. Overall germination at the end of 40 days was 96% for preconditioned seeds and 44% for untreated seeds.

Two additional tests were made. First, seeds were sown on filter paper immediately after collection from a mature capsule (*Perry* 1890a, Oglethorpe Co., Ga.). Of 450 seeds, 67% germinated in 40 days. Second, seeds (*Perry* 1303a) which had been stored for two years at 74°F were sown; 58% germinated of 300 seeds. These germination tests show that a period of preconditioning at low temperatures enhances the rate and percentage of germination, but after-ripening is not necessary for germination. Seedlings grown

in the greenhouse, however, will not elongate unless subjected to low temperatures for three or more months.

Flowering is in July and August. Once an individual has flowered, the plant invariably dies, i.e., it is monocarpic. Efforts to produce additional growth from the roots failed. Under greenhouse conditions mature seeds are released three months after pollination. About 500 seeds per capsule are produced by artificial pollination.

Sabatia quadrangula Wilbur, Rhodora 57: 22. 1955.

Corolla white. Calyx lobes less than 0.5 mm wide. Lower cauline leaves usually oblong, infrequently ovate, often strongly clasping. Lower portion of stem strongly 4-angled, the corners membranous.

Sabatia quadrangula is distributed from southeastern Virginia to central Florida. It is found more frequently in the Piedmont of North and South Carolina than in the Coastal Plain. Plants grow in fields and pinelands, along borders of pocosins, in sandhills, in savannas and flatwoods and in shallow islands of soil on granite outcrops.

Sabatia quadrangula is biennial. A large population occurs on the Anglin Farm granite outcrop in Walton Co., Georgia. Collections were made there in July, 1965, and again in 1966. On both occasions numerous rosettes, identical with the persistent rosettes of flowering specimens, were found. Efforts to transplant these were unsuccessful. The developmental sequence as outlined for *S. angularis* is apparently the same in *S. quadrangula*. Plants are monocarpic. Flowering occurs from mid-June through early July. Fully developed seeds are released about three months after pollination under greenhouse conditions. About 400 seeds per capsule are ordinarily produced by artificial pollination.

Sabatia brachiata Ell., Sk. Bot. S.C. & Ga. **1**: 284. 1817.

Corolla pink (rarely white). Calyx lobes less than 1 mm wide. Lower cauline leaves oblong or elliptic, not strongly clasping. Lower portion of stem terete.

Sabatia brachiata grows from eastern Virginia into Georgia and westward to southern Missouri and Louisiana.

Typical habitats are fields, roadsides, savannas, oak woods, and dry, open pine woods. It is capable of growing in very dry, sandy areas or in low, poorly drained pine woods, ditches, and boggy meadows.

The species is biennial and has basically the same maturation pattern as outlined for other members of the subsection. In summer of 1966, rosettes of *S. brachiata* from Pender Co., N.C., were transferred successfully to the greenhouse. One plant under increased photoperiod and a warm temperature regime elongated during the winter and flowered. Rosettes kept under a cool winter regime were much larger and more robust the following spring.

Sabatia brachiata is not strictly monocarpic. In the greenhouse, plants often survived to flower a second time the following year. Flowering is in June and July. Under greenhouse conditions development of seeds from pollination takes about 4 months. About 450 seeds per capsule are produced by artificial pollination.

Subsection C. CAMPESTRES Blake, Rhodora **17**: 56. 1915.

Annuals, with fibrous roots or a well-developed taproot. Branches alternate. Corolla pentapetalous, pink (rarely white). Anthers recoiled or not at pollen release. Stigmatic branches coiled or not at maturity. Calyx tube very prominently 5-nerved. Basal rosette none. Two species. This subsection is treated as a section (see "Taxonomic Relationships").

Sabatia campestris Nutt., Trans. Am. Phil. Soc. n.s. **5**: 197. 1835.

Leaves and calyx lobes thin and membranous. Calyx lobes 2-6 times longer than the calyx tube and exceeded by the corolla lobes. Anthers 3-6 mm long, becoming circinnately recoiled after pollen release. Stigmatic branches over 5 mm long, becoming strongly coiled at maturity.

Sabatia campestris ranges from Illinois and Missouri south through Oklahoma and eastern Texas, and occasionally eastward to Mississippi. Plants occur in fields and prairies and often along roadsides. The soil is usually dry and sandy, although wet grassy bottoms and alluvial plains

furnish good growing conditions as well. Individuals sometimes grow in open woods. Plants under unfavorable growth conditions rarely branch, are much reduced in height, and produce from one to six flowers. When grown in a greenhouse under favorable conditions, there is considerable branching, increased height growth, and production of 18-50 or more flowers.

Flowering is from mid-June through July in most of the range. Plants are strictly monocarpic. Seeds are produced in about four months under greenhouse conditions. The maturing capsules remain green for a considerable time after the plant dies; they eventually turn brown and dehisce while still within the confines of the dried calyx tube. About 750 seeds per capsule are produced by artificial pollination.

Sabatia arenicola Greenm., Proc. Am. Acad. 34: 569. 1899.

Leaves and calyx lobes thick and succulent. Calyx lobes less than twice the calyx tube length and exceeding the corolla lobes. Anthers about 2 mm long, straight or slightly recoiling after pollen discharge. Stigmatic branches 2-4 mm long, becoming merely flattened and recurved at maturity.

Sabatia arenicola is restricted to beaches and dunes from Louisiana westward to Texas and southward into Mexico. The species often grows just behind the fore dunes and on both sides of succeeding dunes. Such individuals are low and form many short, spreading branches and a long taproot. There is a pronounced succulence of leaves and calyx lobes. Under greenhouse conditions, branching is much less profuse and root growth tends to be fibrous. The succulence of leaves and calyx lobes is maintained.

Flowering occurs from mid-June through early July, and the plants are strictly monocarpic. Seeds are produced in about 2 1/2 months in the greenhouse. Both in the field and greenhouse, *S. arenicola* plants die shortly after flowering. The capsules remain green for a longer period, although growth in size ceases. During this time the capsules remain fleshy and the seeds are soft and saturated with

moisture. Eventually the capsule darkens and dries, and the seeds lose their moisture and assume the characteristic dark color. The capsule dehisces while enclosed within the dried calyx tube. About 500 seeds per capsule are produced by artificial pollination.

Subsection D. CAMPANULATAE Blake, Rhodora **17**: 56. 1915.

Annuals or perennials with fibrous roots, a thin taproot, or a perennating caudex. Branches alternate. Flowers pentapetalous; corolla pink or white. Anthers circinnately recoiled after pollen release. Stigmatic branches coiled at maturity. Basal rosette present or not. Four species.

Sabatia campanulata (L.) Torr., Fl. N. & Mid. U.S. 217. 1824.

Perennial, growing from a short branching underground caudex; often with 2 or more aerial stems. Corolla pink (rarely white). Calyx lobes usually more or less equalling the corolla in length. Leaves oblong, narrowly oval, or linear, usually widest below the middle. Rosette formed by new growth during winter, not persisting.

Sabatia campanulata grows in the Coastal Plain from Massachusetts to northern Florida and westward to Louisiana and Arkansas; and locally inland in Tennessee, Indiana, Illinois, Kentucky, and Arkansas. The species grows in bogs and savannas, often in low, poorly drained meadows and marshes, and occasionally along roadsides.

Within the species there is considerable variation in leaf shape, calyx- and corolla-segment lengths, and degree of branch divergence. This led to recognition of a separate species, *S. gracilis* (Fernald, 1932), having linear leaves, smaller flowers, more divergent branches, and a Coastal Plain distribution from Florida to Louisiana and southeastern Virginia. Later, specimens were found with features of both species and Fernald (1937) concluded they should be treated as geographic varieties. Wilbur (1955) was unable to find consistent differences between the two populations and relegated *S. gracilis* to synonymy with *S. campanulata.*

Wilbur's conclusion is supported by my field and greenhouse observations. Leaf shape, calyx and corolla lengths, and branching are strongly influenced by the habitat. Mass collections from populations in Florida revealed that plants growing among dense clumps of grasses in a savanna or meadow assume the appearance of *gracilis*. The leaves are small and linear, the calyx and corolla segments are narrow and short (less than 15 mm long), and the branches are strongly divergent. Such plants are supported by the surrounding grasses and other vegetation and are so lanky as to be incapable of self-support when the vegetation is removed. By contrast, specimens along roadsides and cleared areas in Florida are self-supporting and often branch considerably from the base. The leaves are larger than in savanna plants and are lanceolate to almost ovate in outline. The calyx and corolla segments may be larger (to more than 2 cm). Branching is strongly ascendant and rigid. Greenhouse progeny of the *gracilis* type take on the typical growth form of *S. campanulata*. Thus, there seem to be no genetically-determined morphologically recognizable subpopulations within the species.

Flowering occurs from mid-June through early August. Development and release of mature seeds takes three months or more from pollination. About 700 seeds per capsule result from artificial pollination.

Sabatia stellaris Pursh, Fl. Am. Sept. **1**: 137. 1814.

Annual, with fibrous roots; usually with one main stem having branches borne on the upper half of the stem. Corolla pink (rarely white). Calyx lobes extending 3/4 the length of the corolla. Leaves linear to obovate, usually widest above the middle. Rosette not formed.

Sabatia stellaris grows along the coast from southern Massachusetts to Louisiana and extends inland in Florida and Mexico. The species is confined to salt marshes, adjacent littoral areas, and swales except in Florida, Mexico, and certain Bahama islands.

Wilbur (1955) noted variation similar to that described for *S. campanulata*. Florida specimens tend to be elongate,

wiry, and slender with narrowly linear leaves. Northern individuals are more compact, less branched, and have broadly elliptical leaves. Wilbur concluded that the differences are not sufficiently constant for recognition of subspecific categories. Collections made for the present study support this conclusion. Individuals growing in a partially cleared area in southern Florida were stocky, robust plants resembling northern material in leaf shape and branching. Regardless of their initial site, greenhouse-grown plants when not crowded are sturdy and non-wiry and have non-linear leaves. A number of field collections and observations have provided convincing evidence that relative wiriness and size of leaves are controlled by competition and associated effects. Much of this variation is lost when transplants or seedlings are grown in a uniform environment.

Britton (1905) and Britton and Millspaugh (1920) recognized two species from the Bahamas, the pink-flowered *S. campanulata* and a white-flowered endemic, *S. simulata* Britton. Wilbur (1955) concluded that all Bahamian material is annual and referable to *S. stellaris.* My collections from four islands in the Bahamas failed to reveal any plants which could be referred to the perennial *S. campanulata.* Plants of *S. stellaris* with pink flowers were found on Eleuthera, Grand Bahama, and Great Abaco islands. These occupied inland sandy areas similar to habitats known for the species in Florida. On New Providence white-flowered forms were found almost exclusively, and these were around salt marshes. Contrary to Britton and Millspaugh (1920), occasional specimens with pink-tinged corollas do occur there also.

Since both pink and white forms sometimes grow sympatrically on Great Abaco, extensive population samples were taken. South of Marsh Harbour, in the "whitelands" of Abaco, exclusively white-flowered individuals were found growing in crevices of the very dry aeolian limestone. These were more succulent in appearance than were any others, and they branched profusely from the base. An individual transferred to the greenhouse developed eight erect flowering stems and numerous shorter lateral branches, while

growing to a height of 29 inches. These "whiteland" individuals probably are differentiated ecotypically from their congeners elsewhere on Abaco and on New Providence.

In moist, low roadside ditches northwest of Marsh Harbour toward Green Turtle Cay, numerous individuals were found with flowers ranging from rose through pink and shades of pink to white. In addition to color, the pattern of the floral "eye" varied. Usually in *S. stellaris* the yellow color at the base of each petal is bordered by an irregular line of maroon or brown color. The border occasionally is lacking. Combinations of these characters were found in the roadside population. A sample of 108 plants was taken and sorted according to floral variation. Forty-seven individuals were found which were florally intermediate between pure white and pink forms. Twenty-seven of these had a strip of white parallel to the border of the "eye." This variation was probably the result of crossing and backcrossing among ancestral populations and suggests that there is no basis for distinguishing *S. simulata*. To study this problem further, white-flowered Bahamian forms were incorporated into the cytological and hybridization programs.

In southern Florida, plants flower throughout the year; elsewhere the flowering time is July and August. Bahamian plants are at a flowering peak in April and May. Seed development takes about two months. An average of 600 seeds per capsule are produced from artificial pollination.

Sabatia grandiflora (A. Gray) Small, Fl. SE. U.S. 928. 1903.

Annual with fibrous roots. Usually one rigid stem with branches confined to the upper third or half of the stem. Corolla pink (rarely white). Calyx lobes mostly less than 3/4 as long as corolla, rarely exceeding it. Leaves rigid, fleshy, those above usually not exceeding the stem in diameter. Lowermost leaves sometimes clustered.

Sabatia grandiflora grows in peninsular Florida and western Cuba. In Florida it grows in the Everglades, in pinelands, along moist sandy roadsides, and along sandy shores of lakes and ponds.

In the greenhouse the lower leaves are not clustered unless the plant has been subjected during early growth to a period of lower temperatures. Individuals growing in standing water in the field frequently have clustered lower leaves.

Flowering occurs primarily in June and July, but occasional flowering specimens have been collected from January through November. Development and release of mature seeds takes two to three months from pollination. Artificial pollination results in about 1100 seeds per capsule.

Sabatia brevifolia Raf., Atlant. Jour. 1: 147. 1832.

Annual, with a slender branching taproot. One main stem, in robust specimens branching nearly to the base; branches usually alternate and widely divergent, giving a wiry appearance. Corolla white. Calyx lobes about 1/2 as long as corolla, or less. Leaves thin, membranous, above often less than 1 mm wide, below variously shaped and to 7 mm wide. Lowermost leaves broader, forming a rosette and often persisting.

Sabatia brevifolia is distributed from southeastern South Carolina throughout Florida and westward to Alabama. It grows in savannas, pinelands, occasionally in moist to wet sandy peat of bogs, and in the dry white sand border of Florida "scrub islands."

This is the only species known to flower exclusively in late summer and early fall. Flowers are produced from mid-August through mid-October in the northern part of its range and through mid-November in southern Florida. The capsules are mature about three months after pollination. About 200 seeds per capsule are produced by artificial pollination. It is not certain whether germination occurs in the fall or spring. Young seedlings form a rosette which often persists to maturity; the plants are strictly monocarpic.

Subsection E. DODECANDRAE Wilbur, Rhodora 57: 78. 1955.

Perennials, with rhizomes. Branches usually alternate. Flowers pluripetalous (in *S. calycina* 5- to 7-merous), pink

(rarely white). Anthers recurved or circinnately recoiled after pollen release. Stigmatic branches recurved or coiled at maturity. Basal rosette present or not. Four species.

Sabatia calycina (Lam.) A. Heller, Bull. Torr. Bot. Club **21**: 24. 1894.

Usually 5-6 corolla lobes (rarely 7). Calyx lobes about as many, foliaceous. Leaves broad, spatulate, tapering to an almost petiolate base, considerably broader than the stem. Rosette none.

Sabatia calycina grows along the Coastal Plain from southeastern Virginia throughout most of Florida, westward to eastern Texas, and in eastern Cuba and central Hispaniola. The species is abundant in the marginal zones of freshwater marshes; it occurs also in moist to swampy lowland hardwood stands, in swamps, in ditches, and often on creek or river banks.

Sabatia calycina was placed by Blake (1915) in his subsection *Campanulatae*, composed of species having flowers with 5 (rarely 6 or 7) petals. My hybridization evidence supports this placement (see "Taxonomic Relationships"). Wilbur (1955) put the species in subsection *Dodecandrae*. There is considerable morphological evidence in support of this. *Sabatia calycina*, in common with the *dodecandra* alliance, has foliose calyx lobes, broad leaves, and a rather leafy seedling. Individuals not excessively branched are much like *S. dodecandra* var. *foliosa*. However, the flowers are smaller and often pentapetalous.

The behavior of stigmatic branches and of anthers at maturity differs from that of other members of the *Dodecandrae* and from the *Campanulatae* as well. The anthers of *S. calycina* become only slightly recurved after pollen release, and the stigmatic branches spread parallel to the upper surface of the flower at maturity. Other species in the *Dodecandrae* possess anthers which become strongly circinnately recoiled after pollen release, and the stigmatic branches become coiled into three or more loops.

Sabatia calycina flowers from early June through July throughout most of its range. Under greenhouse conditions

mature seeds are released three to four months after pollination. Approximately 1000 seeds per capsule are produced by artificial pollination.

Sabatia dodecandra (L.) BSP., Prel. Cat. N.Y. 36. 1888.

Usually 9-12 corolla lobes. Calyx lobes about as many, from inconspicuous to large and foliaceous. Cauline leaves mostly elliptic to oblong, broader than the stem. Rosette formed during winter dormancy, its leaves similar to the cauline leaves.

Two varieties of the species were recognized by Wilbur (1955). *Sabatia dodecandra* var. *dodecandra* grows in brackish marshes from Connecticut into South Carolina and locally in Florida. Each internode exceeds the leaf by 1.5 to 3 times. Stolons are rarely present. Flowering occurs from late June through mid-August, rarely as late as November. In the greenhouse mature seeds are released two to three months from pollination. About 500 seeds per capsule are produced by artificial pollination.

Sabatia dodecandra var. *foliosa* (Fern.) Wilbur grows on river banks and along ponds and streams inland from South Carolina into northern Florida and westward to Louisiana. It may be found in swamps, wet grassy ditches, and low pinelands. The internode is equalled or exceeded by the leaf. Stolons are usually present. Flowering is from mid-June through August. Development and release of mature seeds takes three to four months from pollination. About 2400 seeds per capsule are produced by artificial pollination.

Two other species have been recognized in the *S. dodecandra* complex. Small (1903) proposed *S. harperi*. Blake (1915) concluded that *S. foliosa* (= *S. dodecandra* var. *foliosa* (Fern.) Wilbur) and *S. harperi* Small were conspecific. At the same time Blake (l.c.) described *S. obtusata*. Wilbur (1955) relegated *S. obtusata* Blake to synonymy as a minor variant of *S. dodecandra* var. *foliosa*. The present study has provided no evidence to support recognition of *S. harperi* and *S. obtusata*.

Sabatia kennedyana Fern., Rhodora 18: 150. 1916.

Usually 9-12 corolla lobes. Calyx lobes about as many,

linear and flat, hyaline-margined. Cauline leaves linear to oblanceolate, long-tapering to the base, broader than the stem. Primary branches mostly opposite. Rosette formed during winter dormancy, its leaves similar to the cauline leaves.

Sabatia kennedyana grows from Nova Scotia to South Carolina. In Canada it is found in fresh-water marshes. In the United States *S. kennedyana* grows in eastern Massachusetts, Rhode Island, southeastern North Carolina, and northeastern South Carolina. The species is limited to very wet areas on the Coastal Plain; it is usually found along the margins of ponds and streams or in wet cypress bottomland adjacent to a river or stream. Early growth often takes place under standing water, and the lower half or more of the stem may be submerged. Stolons are usually present.

The species flowers from mid-June through July in North and South Carolina. In Massachusetts, Rhode Island, and Nova Scotia, plants flower from mid-July through August and sometimes later. Development and release of mature seeds take about three months from pollination. About 1300 seeds per capsule are produced by artificial pollination.

Sabatia bartramii Wilbur, Rhodora 57: 91. 1955.

Usually 10-12 corolla lobes. Calyx lobes about as many, usually succulent and rounded in cross-section, strongly subulate. Cauline leaves narrowly linear, less than to slightly broader than the diameter of the stem, thickened. Rosette leaves broadly spatulate, thickened.

Sabatia bartramii grows in southern Georgia and Alabama, throughout Florida, and to southeastern Mississippi. Typical habitats include savannas, low pine barrens, moist roadside ditches, and cypress lowlands. Plants often grow in standing water.

Flowering occurs from mid-June (sometimes earlier in southern Florida) through mid-August. Development and release of mature seeds take three months from pollination.

Approximately 1300 seeds per capsule are produced by artificial pollination.

Section II. PSEUDOCHIRONIA Griseb., Gen. et Sp. Gent. 125. 1839.

Perennials. Branches opposite or alternate. Flowers nearly sessile, if more than one, capitate; 7-12 parted; pink. Bracts subtending flowers large and leaf-like. Anthers never becoming revolutely coiled or strongly recurved after pollen release, instead remaining erect and rigid, sometimes slightly twisted laterally. Stigmatic branches somewhat recurved at maturity. Two species.

The two species placed in this section, *S. capitata* and *S. gentianoides*, are strongly differentiated from other members of the genus and are easily distinguished from each other. Neither species is an annual as reported (Wilbur, 1955). Some individuals of both species were found to have the previous year's dead stem and fruits still attached. Small rosettes of *S. gentianoides* were often present with flowering specimens in the field. Several of these, transferred to a greenhouse, flowered the following year.

Sabatia capitata (Raf.) Blake, Rhodora **17**: 54. 1915.

Basal and cauline leaves not strongly dimorphic, the cauline elliptic or oblong, usually obtuse; the basal similar or broader and shorter. Calyx lobes linear, often unequal, erect.

Sabatia capitata has the most restricted range of any species in the genus. It is known now in northwestern Georgia, although in the 19th century its range extended into southeastern Tennessee, northeastern and central Alabama, and perhaps to southwestern North Carolina. Prior to this study, only three collections of the species had been made after 1900, one from Alabama, the others from Georgia.

Sabatia capitata grows in open hardwoods on moderately dry hillsides and ridges, or occasionally in moist lowland woods. Plants used in this study were collected along the crest of Pigeon Mountain in Walker Co., Georgia. There they grew scattered in open patches of ground in an oak-

hickory stand. Doctor Philip F.-C. Greear of Shorter College has located a disjunct population growing in silicious chert in Bartow Co., Georgia; a limited number of plants were removed for study.

Flowering occurs from late June through mid-August. A period of 2 1/2 to three months from pollination is required for development of mature seeds. About 750 seeds per capsule are produced by artificial pollination.

Sabatia gentianoides Ell., Sk. Bot. S.C. & Ga. **1:** 286. 1817.

Basal and cauline leaves strongly dimorphic, the cauline narrowly linear, width equal to or less than the diameter of the stem; the basal broad, oblong to orbicular spatulate. Calyx lobes subulate, the tips usually reflexed.

Sabatia gentianoides ranges from North Carolina into Florida and westward into eastern Texas on the Coastal Plain. It grows chiefly in savannas and pinelands, occasionally in open bogs, boggy meadows, roadside ditches, and on dry roadside banks.

In North Carolina the species has peak flowering in August, beginning sometimes in mid-July and extending occasionally to mid-October. To the south, flowering is at its peak in July. Development of mature seeds in a greenhouse takes two to three months from pollination. About 1200 seeds per capsule are produced by artificial pollination.

BREEDING SYSTEMS

All species of *Sabatia* are self-compatible. Apomixis is ruled out since emasculated flowers fail to set seed and artificial hybrids combine traits of both parents. While all species are capable of autogamous reproduction, the majority are protandrous. The difference in time between stigmatic receptivity and anther dehiscence varies with the species, and dichogamy may be partial to complete. Outcrossing is favored also by physical separation of the stigma and anthers. In most species the filaments, which were erect at pollen release, bend toward the corolla and away from the expanding stigmatic branches. It thus becomes unlikely that any remaining pollen could be transferred by mechanical means to the stigma.

In *S. difformis* and *S. macrophylla* the outermost flowers in the cymules mature last and are frequently staminate. A small ovary and style may be present, but the stigmatic lobes never extend above the corolla tube. Staminate flowers have not been observed in the other species. A loss of vigor which accompanies end-of-season flowering accounts for the staminate expression; its effect on outcrossing is probably negligible.

The breeding system was studied in the field and greenhouse. Table 1 summarizes floral maturation data obtained from plants growing under uniform conditions in a greenhouse. Observations were made concurrently on all species, except *S. brachiata*, during a time of consistently warm, clear weather. The overall developmental sequence is slowed somewhat by cloudy or cool weather, or both, but successive events seem to be relatively constant.

Full release of pollen from mature anthers takes less than 24 hours, but some pollen may adhere for longer periods. After dehiscence the anthers become dry and often drop from the filaments. In seven species this occurs one or two days before the stigmatic branches are receptive. Eight species show partial overlap in stigmatic receptivity and presence of pollen. However, the stigmata are never receptive, or even uncoiled, on the same day that pollen is fully released. In the field, where wind and insects will shake the flowers and remove pollen, it is less likely that pollen will be left at the time stigmatic branches are receptive.

The comparatively unrelated *S. calycina* and *S. arenicola* are not protandrous. Stigmatic surfaces are receptive on the same day pollen is fully released. Floral structures are such that the stigmatic branches are invariably brought into contact with the dehiscing anthers and autogamy is assured. Seed set by both species is high. Prevention of pollen transfer by wind or by insects does not affect seed set.

Moore and Lewis (1965) have shown that the evolution of self-pollination frequently is associated with morpholog-

TABLE 1

Sequence of events in anthesis of *Sabatia* flowers. Values are given in consecutive days. The first day in each case is that on which expansion of the flower bud began.

Taxa	Developmental Sequence							
	Bud Opening	Petals Extended	Anthers Recurving	Anthers Dehiscent	Pollen Shed	Stigma Uncoiling	Stigma Receptive	Maturation Overlap
Section *Sabatia*								
Subsect. *Difformes*								
S. difformis	1	2	2	3	5	6	7	none
S. m. var. *macrophylla*	1	2	2	2 - 3	4	5	6	none
S. m. var. *recurvans*	1	2	2	3	4	5	6	none
Subsect. *Angulares*								
S. angularis	1	2	1	2	7	4	5	partial
S. brachiata	1	2	2	3 - 4	8	6	7	partial

Subsect. *Campestres*								
S. campestris	1	2	2	3	7 - 8	7	8	partial
S. arenicola	1	2	2	3	6	2	3	complete
Subsect. *Campanulatae*								
S. campanulata	1	2	2	3	4 - 5	5	6	none
S. stellaris	1	2	2	3	4	4	5	none
S. grandiflora	1	2	2	3	7	5	6	partial
Subsect. *Dodecandrae*								
S. calycina	1	2	2	3	7	2	3	complete
S. d. var. *dodecandra*	1	2	2	3	5	5	6	none
S. d. var. *foliosa*	1	2	2	3	6	4	5	partial
S. kennedyana	1	2	2	3	5 - 6	4	6	partial
S. bartramii	1	2	2	3	7	5	6	partial
Section *Pseudochironia*								
S. capitata	1	2 - 3	–	4	8 - 9	5	6	partial
S. gentianoides	1	2	–	2 - 4	5	5	7	none

ical and cytogenetic differentiation. There is relaxed selection for conspicuous flowers and positive selection for smaller flower parts, excluding the ovary. However, the essential change is either early maturation of the stigma (Moore and Lewis, l.c.) or retarded anther dehiscence (Breese, 1959). A reduction in chromosome number is generally correlated with simplification of the life cycle, reduction in size, and increase in uniformity of the breeding system (Grant, 1956a).

Additionally, an autogamous breeding system is most likely to arise in annuals or short-lived perennials which inhabit temporary or marginal areas (Stebbins, 1957; Moore and Lewis, 1965). Abundant seed production from year to year is assured, and ". . . the descendants of a single well-adapted initial colonizer will be equally well-adapted to these same conditions . . ." (Stebbins, 1957). Self-pollination is also advantageous when environmental conditions reduce pollinator activity (*cf.* Haskell, 1953; Ornduff, 1966).

These correlated responses are associated with the autogamous breeding system in *Sabatia*. *Sabatia arenicola* is a small monocarpic annual which is restricted to beaches and dunes. The flowers are reduced in size; the ovary, however, is large. Stigmatic branches are receptive when the anthers dehisce, and mechanical transfer of pollen is assured by the proximity of anthers and stigmas. The chromosome number ($n=14$) is one of the lowest in the genus, and the developmental cycle one of the shortest.

Sabatia calycina is a polycarpic short-lived perennial. The plant is somewhat reduced in size, and flowers are smaller than are those of other members of subsection *Dodecandrae*. It is capable of flowering the first year. Stigmatic branches are receptive when the anthers dehisce, and there is mechanical transfer of pollen. The paludal habitats of this species may be stable or, if by moving water, unstable. It has a polyploid chromosome number ($n=32$).

Evolution of the inbreeding system in *Sabatia* appears to have been favored by positive selection for early maturation of the stigma. Associated morphological parallelisms,

such as reduction in flower size, have evolved, though outcrossing is not structurally prohibited. Thus, there is a degree of breeding duality which can meet the conflicting demands of immediate fitness and long-term flexibility and which is adaptively beneficial under varying environmental stresses.

POLLINATORS

Published reports and my field observations show that the larger-flowered outcrossing Sabatias are pollinated primarily by bumblebees *(Bombus)* and that the smaller-flowered species, incapable of supporting the weight of a bumblebee, are visited by lighter bees (often of family Halictidae). Species of *Bombus* (family Apidae) were collected from flowers of *S. bartramii* (*Bombus impatiens* Cresson) and of *S. capitata* (*B. pennsylvanicus* [DeGeer]). Pollen grains of *Sabatia* were found in the corbiculae of each bee. There appears to be a certain amount of flower inconstancy, since pollen grains of other species were found with those of *Sabatia*.

Augochloropsis metallica metallica (Fabricius), family Halictidae, was collected from *S. kennedyana* and *S. macrophylla* var. *recurvans*. Collections of *Halictus* sp. (Halictidae) were made from *S. campanulata*, and pollen from the insects' bodies resembled that of *S. campanulata*.

Coleopteran visitors included *Phyllophaga rugosa* (Melsheimer), family Scarabaeidae; cf. *Anisosticta*, family Coccinellidae; and *Epicauta* cf. *lemniscata* (Fabricius), Meloidae. *Sabatia* pollen grains in most instances were found on the mouthparts. The flower spiders *Xysticus* sp. and *Misumenoides aleatorius* (Hentz) are commonly associated with *S. macrophylla* but do not aid in cross-pollination.

Mitchell (1960, 1962) listed three additional species of *Sabatia* pollinators. With revised nomenclature the flower records were attributed to Robertson (1929) whose collections were made from *S. angularis*. Robertson identified *Ceratina (Zadontomerus) dupla dupla* Say, Xylocopidae; cf. *Augochlorella aurata* (Smith), Halictidae, as *Oxysto-*

glossa similis; and *Megachile (Litomegachile) brevis brevis* Say, Megachilidae.

A detailed description of floral adaptation for pollinators is given by Hill (1891) for *S. angularis.* He reported that the anther walls are stretched as the anther recurves, and that pollen is forcibly released when the anther is grasped or pressed by the legs of an insect. Robertson (1929) considered the flower of *S. angularis* to be a "non-social long-tongued bee flower."

Floral records of bees (Mitchell, 1960; 1962) indicate that the species reported here are polylectic. They are known to gather pollen from a variety of plant groups, not exclusively from *Sabatia.* As opposed to oligolectic bees which visit specific plant groups for pollen, polylectic bees often are nectar-seeking (Raven, 1962) and will visit younger flowers with dehiscing anthers as well as older flowers which have receptive stigmata.

CHROMOSOME NUMBERS

The first chromosome numbers in *Sabatia* were published by Lewis, Stripling, and Ross (1962) who reported counts for *S. campestris* of $n=13$ (Brazos Co., Texas) and $2n=26$ (Nacogdoches Co., Texas). Bostick (1965) reported $n=14$ for *S. brachiata* (Pender Co., N.C.). Over 70 populations have now been sampled and chromosome counts made for all species in the genus.

Chromosome numbers were determined from buds collected in the field or from plants grown in a greenhouse. Counts were made from pollen mother cell preparations at metaphase I of meiosis. No report is based on an average or on a single observation. Buds were fixed in acetic alcohol (1:3) or in acetic alcohol chloroform (1:3:6); the addition of chloroform was found to enhance cytoplasmic staining and was discontinued. Buds collected from greenhouse material were placed in the fixative and refrigerated for 12 hours. The buds then were rinsed and stored in 70% ethanol under refrigeration. Field collections were refrigerated as soon as possible. Staining was done with acetocarmine. Most species presented no staining difficulties,

but *S. kennedyana* chromosomes usually were not very selectively stained with the standard techniques.

The hour of the day at which buds were fixed had no noticeable effect on the number of metaphase I figures observed. Buds ordinarily were collected from greenhouse material between the hours of 7:00 and 11:00 A.M. There is a correlation between anther size and developmental stage of the pollen tetrad although this varied somewhat with time of year and the individual plant's vigor. The five anthers of pentapetalous species had synchronous meiotic divisions. In pluripetalous species having 8 or more anthers, tetrad development was successive from anther to anther rather than simultaneous.

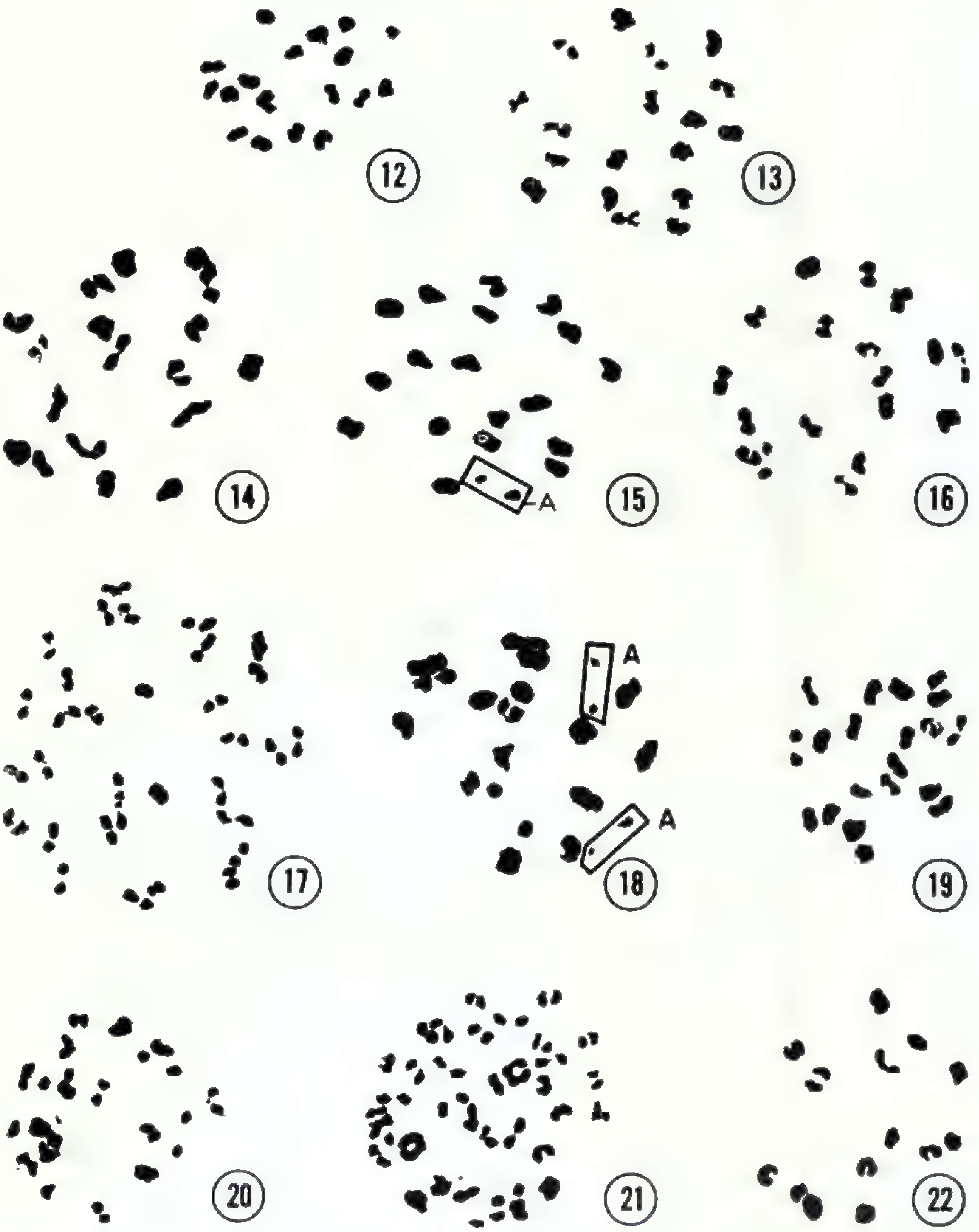
All observations and photographs were made from freshly stained preparations. Photographs were taken at ×1500 with a Leitz Ortholux microscope (90X objective, N.A. 1.32, 10× ocular) and Kodak Contrast Process Ortho film. Photographs were reduced to ×1000 for publication. Voucher specimens are deposited in the Duke University Herbarium.

The count of $n=13$ for *S. campestris* (Lewis et al., 1962) was confirmed. My findings for *S. brachiata* ($n=16$), based on six individuals from two populations, do not agree with the $n=14$ count by Bostick (1965). Both reports are based on samples from the same county; such variation seems unlikely but not impossible. As a result of the present study a wide array of chromosome numbers for the genus is now known: $n=13$, 14, 16, 17, 18, 19, 20, 32, and 38. Various morphological types have developed at the different ploidal levels; in addition, two aneuploid races are known in a single species, *S. quadrangula* ($n=16$, 17). Some gametic complements are pictured in Fig. 1-22, and counts are summarized below. Collection numbers are mine unless otherwise specified.

S. difformis ($n=18$). N.C.: BRUNSWICK CO., 1 mi S of Longwood, 1293. 8 mi W of Leland, 1298. PENDER CO., 1 mi N of Watha, 1881. S.C.: JASPER CO., N of Grays, 1690. Fla.: SANTA ROSA CO., E Bank of Blackwater River at Milton, 1665.

S. macrophylla var. *macrophylla* ($n=19$). Fla.: SANTA ROSA CO.,

Figs. 1-11. Meiotic chromosomes of *Sabatia*. ×1000. Fig. 1. *S. difformis, Perry* 1881, $n=18$. Fig. 2. *S. macrophylla* var. *macrophylla, Perry* 1449, $n=19$ (nucleolus, N). Fig. 3. *S. macrophylla* var. *recurvans, Perry* 1650, $n=19$. Fig. 4. *S. angularis, Perry* 1303, $n=19$. Fig. 5. *S. brachiata, Perry* 1884, $n=16$. Fig. 6. *S. quadrangula, Perry* 1655, $n=16$ (nucleolus, N). Fig. 7. *S. quadrangula, Perry* 1655, $n=16$ (nucleolus, N). Fig. 7. S. *quadrangula Perry* 1455, $n=17$. Fig. 8. *S. arenicola, Perry* 1425, $n=14$. Fig. 9. *S. campestris, Perry* 1429, $n=13$. Fig. 10. *S. brevifolia, Perry* 1696, $n=16$. Fig. 11. *S. campanulata, Perry* 1391, $n=17$.



Figs. 12-22. Meiotic chromosomes of *Sabatia*. ×1000. Fig. 12. *S. grandiflora, Stone* 1671, $n=18$. Fig. 13. "*S. simulata,*" *Perry* 1637, $n=18$. Fig. 14. S. *stellaris, Perry* 1294, $n=18$. Fig. 15. *S. stellaris, Perry* 1517, $n=18$ (accessory chromosomes, A). Fig. 16. *S. bartramii, Perry* 1443, $n=18$. Fig. 17. *S. calycina, Stone* 1648, $n=32$. Fig. 18. *S. dodecandra* var. *dodecandra, Wilbur* 8475, $n=17$ (accessory chromosomes, A). Fig. 19. *S. dodecandra* var. *foliosa, Perry* 1678, $n=19$. Fig. 20. *S. kennedyana,* Perry 1694, n=20. Fig. 21. *S. capitata, Perry* 1661, $n=38$. Fig. 22. *S. gentianoides, Perry* 1670, $n=14$.

10.5 mi N of Holley, 1449. **Miss.**: STONE CO., Univ. of Miss. forestry camp, 1389.

S. macrophylla var. *recurvans* (*n*=19). **Ga.**: CHARLTON CO., 12 mi S of Folkston, 1650, **Fla.**: COLUMBIA CO., 5.4 mi W of Olustee, 1685.

S. angularis (*n*=19). **N.C.**: DURHAM CO., 2.4 mi E of Catsburg, 1303. **Ga.**: OGLETHORPE CO., 16 mi NE of Lexington, 1890. **Md.**: CALVERT CO., 1 mi W of Chesapeake Beach, 2021.

S. quadrangula (*n*=16, 17). **N.C.**: DURHAM CO., 2.2 mi E of Catsburg, 1655 (*n*=16). **Ga.**: WALTON CO., Anglin Farm granite outcrop, 1886 (*n*=17). **Fla.**: CALHOUN CO., 1.4 mi E of Clarksville, 1455 (*n*=17).

S. brachiata (*n*=16). **N.C.**: PENDER CO., 3 mi S of Burgaw, 1300. 4 mi S of Burgaw, 1884.

S. campestris (*n*=13). **Texas**: HARDIN CO., S of Sour Lake, 1429.

S. arenicola (*n*=14). **Texas**: GALVESTON CO., Jamaica Beach, S of Galveston, 1425. Galveston Beach, 1427.

S. *campanulata* (*n*=17). **Tenn.**: CARTER CO., Hunter Bog at Hunter, E of Elizabethton, 1659. **N.C.**: PENDER CO., 1 mi N of Watha, 1882. **Ga.**: BARTOW CO., 4.5 mi SE of Adairsville, 1663. **Fla.**: COLUMBIA CO., 7.8 mi W of Olustee, 1684. **Miss.**: STONE CO., Univ. of Miss. forestry camp, 1391.

S. stellaris (n=18; including "*S. simulata*" from Bahamas). **N.C.**: BRUNSWICK CO., Caswell Beach, 1294. CARTERET CO., Shackleford Bank, 1478. DARE CO., Outer Banks, near road to Manteo, 1656. **Fla.**: BROWARD CO., W of Deerfield, 1567. COLLIER CO., 7.1 mi E of Monroe Station, 1517. TAYLOR CO., N edge of Aucilla Wildlife Management Area, *B. J. Moore, s.n.* **Eleuthera Island**: N end, E of Current, 2038. S end, N of Davis Harbour, 2040. NE of Preacher's Cave, 2043. **Great Abaco Island**: SW of Marsh Harbour near pulpwood plant, 1777. SW of Marsh Harbour, 1779. In "whitelands" 3 mi W of Owens-Illinois pulpwood plant, 1784. NW of Marsh Harbour, toward Green Turtle Cay, 1799. **New Providence Island**: marsh S of Carmichael Village, S coast, 1637.

S. grandiflora (*n*=18). **Fla.**: BAY CO., SE shore of Lake Merial, *D. E. Stone* 1452. COLLIER CO., Everglades, N of Loop Road at Pinecrest, 1555. HIGHLANDS CO., W of Kissimmee River along Fla. route 70, *D. E. Stone* 1671. LAKE CO., W of Sorrento, 1682.

S. brevifolia (*n*=16). **S.C.**: COLLETON CO., 3 mi W of Smoaks, 1696. **Fla.**: COLLIER CO., 7.5 mi NW of Immokalee, *O. Lakela* 30216. HILLSBOROUGH CO., Univ. of South Florida campus, *R. W.* and *K. Long* 2013. LEVY CO., between Bronson and Otter Creek, *B. J. Moore s.n.* SUMTER CO., between Rutland and Wildwood, *B. J. Moore s.n.*

S. calycina (*n*=32). **N.C.**: BRUNSWICK CO., SW of Wilmington, 1296. **Fla.**: COLLIER CO., W of Collier Co. Scenic Rd., 1539. OSCEOLA CO., 0.5 mi W of Brevard Co.-Osceola Co. line, *D. E. Stone* 1648.

S. dodecandra var. *dodecandra* (n=17 + 4 accessory chromo-

somes). **N.C.**: CARTERET CO., 13 mi N of Beaufort toward South River, 1885. *R. L. Wilbur* 8475.

S. dodecandra var. *foliosa* (n=19). **S.C.**: JASPER CO., 5.4 mi S of Ridgeland, 1689. **Ga.**: ATKINSON CO., 14 mi S of Pearson, *S. A. Earle* 65112. **Fla.**: HAMILTON CO., E of Jasper, 1683. JEFFERSON CO., 2.3 mi W of Lamont, 1458. LAFAYETTE CO., Steinhatchee Wildlife Management Area, 1678. SANTO ROSA CO., E bank of Blackwater River at Milton, 1666.

S. *kennedyana* (n=20). **Mass.**: BARNSTABLE CO., E bank of Cedar Lake, Cape Cod, 1694. **S.C.**: HORRY CO., just E of Waccamaw River, 1875.

S. bartramii (n=18). **Ga.**: CHARLTON CO., 3.4 mi S of St. George, 1687. **Fla.**: BAY CO., 5 mi E of Panama City, 1672. COLLIER CO., 7 mi E of Monroe Station, 1521. HERNANDO CO., 1 mi NW of Aripeka, 1679. LEVY CO., N of Cedar Key, *B. J. Moore s.n.* SANTA ROSA CO., 10.5 mi N of Holley, 1446. WAKULLA CO., SE of Wakulla, 1675. **Ala.**: BALDWIN CO., 0.7 mi NE of Stapleton, 1443.

S. capitata (n=38). **Ga.**: WALKER CO., Pigeon Mt., SW of Lafayette, 1661.

S. gentianoides (n=14). **Ga.**: CHARLTON CO., 8.3 mi N of St. George, 1688. **Fla.**: WALTON CO., 1.5 mi N of Choctawhatchee Bay, 1670.

Few meiotic irregularities were observed. Chromosomes of *S. dodecandra* var. *dodecandra* and of *S. brachiata* occasionally showed early disjunction. Accessory chromosomes were seen in preparations from one collection of *S. stellaris* from Florida (*Perry* 1517, Fig. 15). Of 50 cells studied from this population, 78% had one or two accessory chromosomes. Only one population of *S. dodecandra* var. *dodecandra* was available for study. Four accessory chromosomes were consistently associated with the 17 pairs in all cells studied (Fig. 18). It is uncertain whether the original number was n=19 (as in *S. dodecandra* var. *foliosa*), and the essential parts of the accessory have been transferred to other chromosomes through translocation, or whether this was a local aberrant population and the usual number is n=19. Other collections of the variety must be made for further study.

As the haploid chromosome number decreases in *Sabatia* there is a tendency toward the annual or biennial habit and a corresponding simplification of morphology. There is a decrease in floral size, number of floral parts, and promi-

nence of leaves. Most of the annuals and biennials are capable of growing in drier habitats. In one annual species (*S. arenicola*, $n=14$) an inbreeding system has been derived as an additional specialization for the annual growth habit. Similar correlations with descending aneuploidy have been recorded in the literature for several genera in other families and, in the Gentianaceae, for *Swertia* (Khoshoo and Tandon, 1963).

POLLEN VARIATION

There appear to be no differences in exine sculpturing among the species. The exine has a granular texture and the wall is about 1.0-2.5 μ thick. The grains are tricolpate and each colpus has a circular germ pore. The aperture membrane is smooth and sometimes protrudes beyond the general outline. In polar view the grains are triangular with rounded apices.

Pollen samples were taken from 88 live plants of 49 populations. Pollen was placed directly in lactophenol-cotton blue; measurements were made about 24 hours after collection. The grains usually were oriented in polar view on the slide. Therefore, all measurements were made from one pore past the polar axis to the wall opposite the pore. Grains distorted or with unequal planes of symmetry in polar orientation were not measured. A Spencer microscope with 10$\times$ oculars and 44$\times$ objective was used for measurements which were made to the nearest optical line (1 division = 1.52 μ).

Since many of these individuals were used in the experimental hybridizations, it was necessary to obtain pollen fertility data in order to establish expected norms of fertility in parental species. Fertility estimates are based on the number of stained grains in a sample of not less than 400 grains from each species.

Combined results of the pollen size measurements and fertility estimates are given in Table 2. There are no consistent correlations of pollen size with chromosome number. Those species with 13 or 14 pairs of chromosomes have grains which are fully as large as grains of species with a

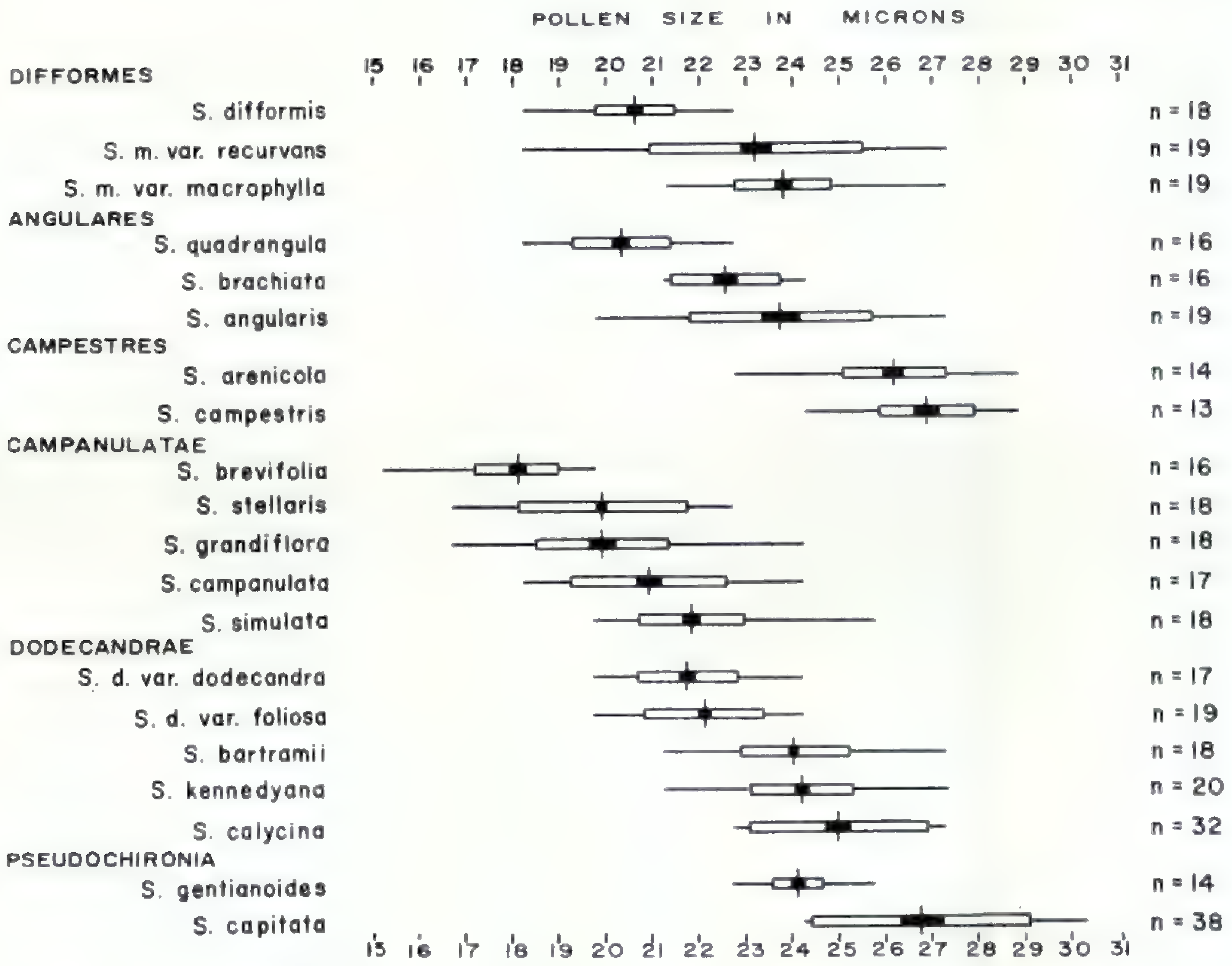


Fig. 23. Pollen size in *Sabatia*. The length of each line represents the range of that set of measurements. A crossbar shows the position of the mean; on each side of the mean the dark line marks two times the standard error and the open rectangle extends for one standard deviation.

higher number of 18 or more pairs. With regard to ranges of means, there seems to be a tendency for members of each subsection to be grouped more closely with one another than with other subsections (Fig. 23). Nonetheless, pollen size is unreliable as an indicator of ploidy and is not useful as a species characteristic.

EXPERIMENTAL HYBRIDIZATIONS

There are no published accounts of either artificial or natural interspecific hybridizations in *Sabatia*. The artificial pollinations reported here were done under similar cultural conditions during two growing seasons. Reciprocal crosses were made among almost all taxa, and an attempt was made to repeat each crossing combination at least ten times using plants from different populations.

TABLE 2

Size and fertility estimates of *Sabatia* pollen (SE, standard error of mean; SD, standard deviation of mean; CV, coefficient of variation).

Taxa	Size in μ					Number Grains Measured	Percent Viable	Number Grains Scored
	Range	Mean	SE	SD	CV			
Section *Sabatia*								
Subsect. *Difformes*								
S. difformis	18.21 - 22.76	20.59	.07	0.85	.04	150	94.6	1400
S. m. var. *macrophylla*	21.25 - 27.32	23.80	.09	1.04	.04	150	97.0	1200
S. m. var. *recurvans*	18.21 - 27.32	23.20	.16	2.29	.10	200	94.2	1400
Subsect. *Angulares*								
S. angularis	19.73 - 27.32	23.75	.20	1.96	.08	100	95.5	900
S. quadrangula	18.21 - 22.76	20.29	.08	1.07	.05	200	92.7	1600
S. brachiata	21.25 - 24.28	22.58	.12	1.17	.05	100	95.7	1200
Subsect. *Campestres*								
S. campestris	24.28 - 28.83	26.89	.14	1.02	.04	50	98.4	500
S. arenicola	22.76 - 28.83	26.21	.11	1.10	.04	100	95.1	800

Subsect. *Campanulatae*								
S. campanulata	18.21 - 24.28	20.93	.14	1.70	.08	150	97.8	400
S. stellaris	16.70 - 22.76	19.94	.05	1.82	.07	650	95.8	5100
"*S. simulata*"	19.73 - 25.80	21.84	.08	1.16	.05	200	93.7	1400
S. grandiflora	16.70 - 24.28	19.95	.12	1.42	.07	150	95.9	900
S. brevifolia	15.18 - 19.73	18.12	.09	0.89	.05	100	96.8	1000
Subsect. *Dodecandrae*								
S. calycina	22.76 - 27.32	25.02	.14	1.97	.08	200	97.4	1600
S. d. var. *dodecandra*	19.73 - 24.28	21.76	.09	1.11	.05	150	97.2	900
S. d. var. *foliosa*	19.73 - 24.28	22.13	.07	1.30	.06	300	95.0	2100
S. kennedyana	21.25 - 27.32	24.24	.07	1.10	.05	250	93.2	2000
S. bartramii	21.25 - 27.32	24.06	.05	1.19	.05	475	96.7	3000
Section *Pseudochironia*								
S. capitata	24.28 - 30.35	26.80	.24	2.35	.09	100	98.5	800
S. gentianoides	22.76 - 25.80	24.13	.08	0.56	.02	50	95.5	400

Approximately 4400 pollinations have been recorded.

Emasculation was accomplished by removing stamens before the stigmatic branches became untwisted and receptive. In *S. arenicola* and *S. calycina* this necessitated opening the flower bud. Removal of petals had no effect on subsequent ovary or seed development. Mature anthers were detached with forceps and used as applicators of pollen to the emasculated female parent.

Foreign pollen was excluded by screening the greenhouse and by enclosing emasculated flowers in glassine envelopes. As a check of contamination, flowers were emasculated as usual and not artificially pollinated. Capsules were examined later for seed set. Fertility controls were maintained by frequent checks of pollen viability and by selfing. Interpopulational crosses gave the same results as those obtained from self-pollinations. As measured by pollen viability and seed set, fertility of all parental plants was high. In no case, however, were the last flowers of a season used in the crossing program.

Ease of crossing may be estimated from the number of hybrid seeds taken from a given number of emasculated and cross-pollinated flowers (Grant and Grant, 1960). Each cross was evaluated in terms of the average number of ovules tested in the female parent. This procedure has proved useful in a number of studies (*see* Borrill, 1958; Ellison, 1964; Taylor, 1965) and was modified from Gillett (1955) and Levin (1966) for use with *Sabatia*. The number of ovules tested was obtained by averaging the number of seeds produced by ten or more self-pollinated flowers of the female parent. It is assumed that, when a flower is selfed with liberal amounts of pollen, the number of seeds released will be equivalent to the number of ovules normally produced by that species. Percentage seed set was derived by dividing the total number of filled seeds obtained in a given series of crosses by the number of ovules tested in the same number of crosses.

Crossability, as used here, means the extent to which hybrid seeds are formed. It is expressed as a percentage of the average ovule production of the pistillate parent.

Since the germination of non-hybrid *Sabatia* seed varies with storage conditions, specific germination percentages for hybrids are not used as a measure of crossability. Relative germinability, however, has been useful in evaluating the crosses. Samples of seed from each crossing combination were sown to verify viability.

The success of crosses, in terms of crossability and interfertility, serves as a test of the validity of taxonomic groupings (Kruckeberg, 1961). In addition, crossability elucidates genetic relationships of the parental species. Lowered crossability may mean a more distant genetic relationship, although the action of a few genes can obscure this (Khush, 1962). Thus, while inability to cross may be at times an unsafe guide to relationship, the use of crossability in the positive sense is not unreliable (Valentine, 1961).

Intrasubsectional and intrasectional crosses in *Sabatia* are summarized in Fig. 24. Lines graphically present the seed set percentage, and the actual value is given for successful crosses. All successful crosses within the genus are shown in Fig. 25. A complete listing is presented in Perry (1967).

1. CROSSES WITHIN SUBSECTIONS OF SECTION SABATIA.

Subsect. DIFFORMES. There is unequal reciprocal crossability between *S. macrophylla* and *S. difformis*. Seed set is reduced when *S. difformis* is used as the pollen parent to either variety of *S. macrophylla*. Differences in style lengths do not account for the discrepancy since the style of *S. macrophylla* is shorter than that of *S. difformis*. Hybrid seeds germinated well but, due to cultural difficulty, no hybrids reached maturity.

Subsect. ANGULARES. Members of *Angulares* have only slight crossability. The n=16 race of *S. quadrangula* showed greater crossing compatibility with *S. angularis* than did the n=17 race. This accounts for the higher value of 8.9% in the *S. angularis* (♀) × *S. quadrangula* crosses in which the n=16 race was incorporated. In the reciprocal, only the n=17 race was used. The n=17 race was used

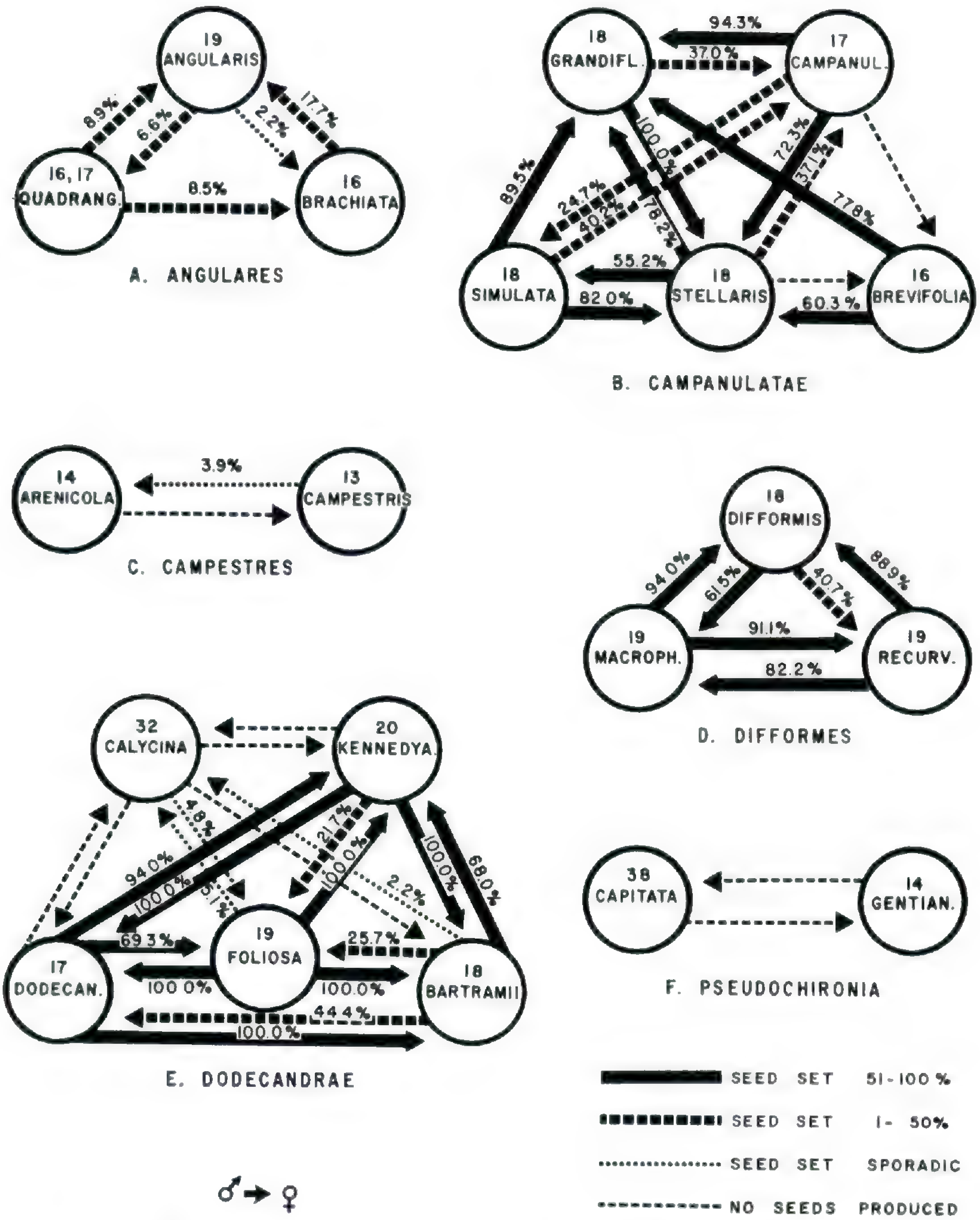


Fig. 24. Crosses within subsections of Section *Sabatia* and within Section *Pseudochironia*. Percentage seed set is given for successful crosses. The gametic chromosome number of each taxon is indicated. A. Crosses among members of Subsect. *Angulares*. B. Crosses among members of Subsect. *Campanulatae*. C. Crosses between members of Subsect. *Campestres*. D. Crosses among members of Subsect. *Difformes*. E. Crosses among members of Subsect. *Dodecandrae*. F. Crosses between members of Section *Pseudochironia*.

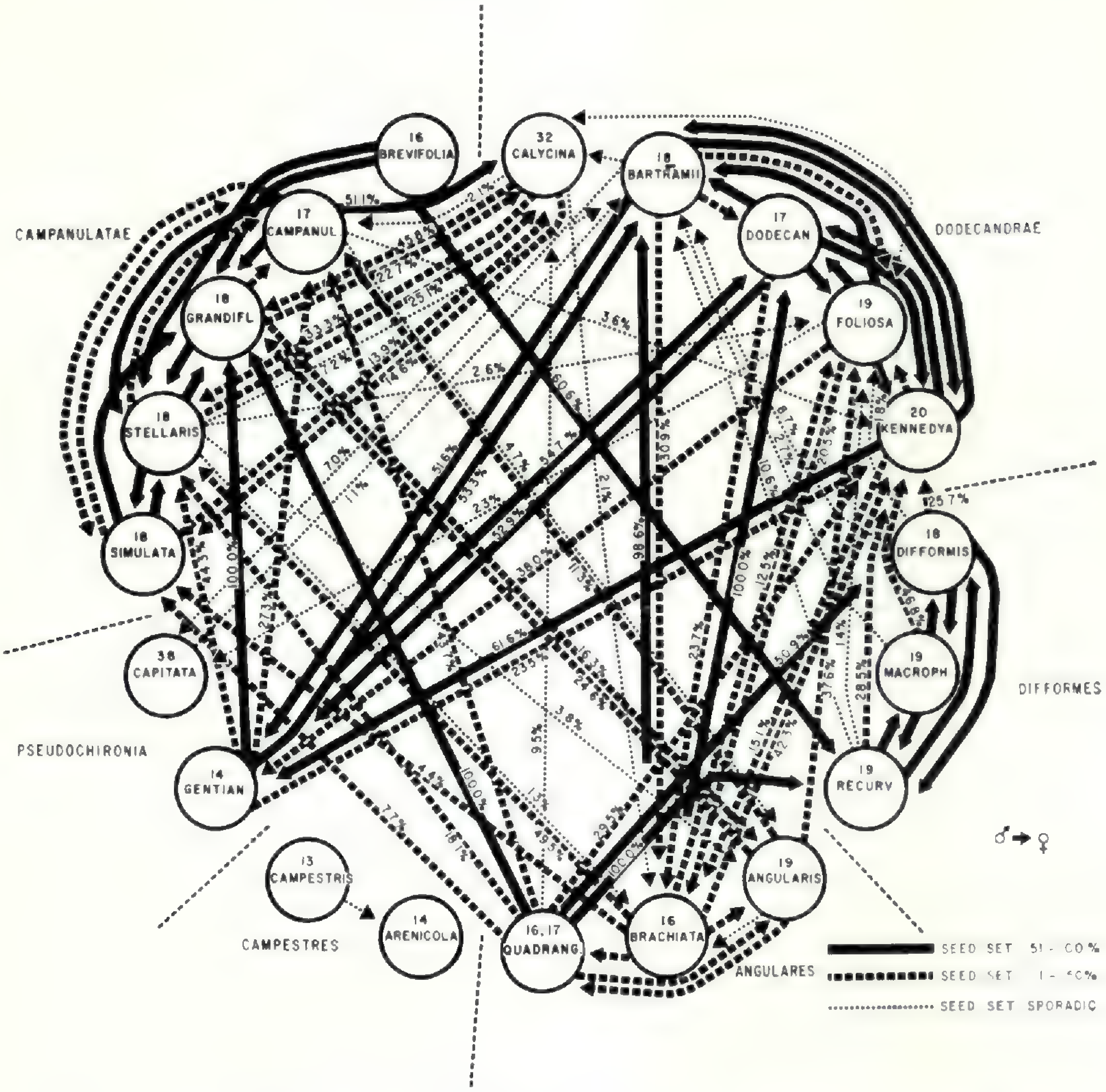


Fig. 25. Summary of successful crosses within the genus *Sabatia*. Percentage seed set is given for intersectional and intersubsectional crosses. The gametic chromosome number of each taxon is indicated.

exclusively in crosses of *S. quadrangula* to *S. brachiata* (n=16) and the value given may be less than would occur in homoploid crosses. In crosses of *S. angularis* and *S. brachiata*, seed set always occurred when *S. angularis* was the pistillate parent. Only one of five crosses resulted in seed set when *S. angularis* was the pollen parent, thus the value of 2.2% does not give positive evidence of crossability. Hybrids were unhealthy and did not reach reproductive maturity.

Subsect. CAMPESTRES. Although 62 attempts were made,

Campestres and *Difformes*, *Campanulatae*, *Dodecandrae*, or *Angulares*.

ANGULARES × DIFFORMES. *Sabatia quadrangula* was found to cross readily as the pollen parent with *S. difformis* and *S. macrophylla* var. *recurvans*, but hybrids did not mature. The reciprocal crosses were not made due to a lack of material of *S. quadrangula*, and no crosses of *S. quadrangula* were made to *S. macrophylla* var. *macrophylla*. Other species of the *Angulares* failed to cross with members of *Difformes*.

CAMPANULATAE × DIFFORMES. *Sabatia brevifolia* as the pollen parent crossed with *S. macrophylla* var. *recurvans*. The former species was not available for additional crosses because of its late flowering. All other crosses failed.

ANGULARES × DODECANDRAE. There was moderate to high crossability of *S. brachiata* with *S. dodecandra* var. *dodecandra* (no hybrid grown), *S. kennedyana* (no hybrid), *S. bartramii* (hybrid sterile; see Table 3), and *S. dodecandra* var. *foliosa* (hybrid fertility low).

Sabatia quadrangula crossed only as the pollen parent with *S. calycina* and *S. kennedyana*. *Sabatia angularis* crossed as the pollen parent with *S. dodecandra* var. *foliosa*.

DODECANDRAE × DIFFORMES. Only *S. kennedyana* crossed as the seed parent with members of the *Difformes*: *S. difformis* and *S. macrophylla* vars. *macrophylla* and *recurvans*. The hybrids from these three crosses were sterile. They resembled the pollen parents by having tightly coiled stigmas and white flowers, but incorporated the yellow floral "eye," larger flower, and increased petal number of the seed parent. The reciprocal crosses gave no positive evidence of crossability. Members of *Difformes* showed slight crossability to *S. dodecandra* var. *foliosa* and to *S. bartramii*.

CAMPANULATAE × ANGULARES. Pollen from each species of the *Angulares* produced seed when crossed with one or more members of the *Campanulatae*. As a seed parent, only *S. angularis* crossed with members of *Campanulatae*. *Sabatia brachiata* crossed exclusively with *S. stellaris*.

The F_1 hybrids from the cross of *S. stellaris* (♀) × *S.*

brachiata were sterile. Of 1300 pollen grains scored from four plants, 1.3% were viable; three of the four plants had no viable pollen. The hybrids were similar in morphology to the pistillate parent.

Hybrids from the cross of *S. stellaris* (♀) × *S. quadrangula* are also available (Table 3). The hybrids had white corolla lobes tinged with pink on the underside. The petals were rather broadly spatulate and the yellow floral "eye" of *S. stellaris* was present. In addition to having white corollas, the hybrids resembled the pollen parent by having opposite branches, broad leaves, and an angular stem. The calyx lobes usually exceeded those of the corolla.

Hybrids of *S. grandiflora* (♀) and *S. campanulata* (♀) with *S. angularis* were not vigorous. Vegetatively they resembled the pistillate parent.

Dodecandrae × Campanulatae. It is significant that only *S. calycina (Dodecandrae)* crossed freely with all members of the *Campanulatae* except *S. brevifolia. Sabatia kennedyana* possibly crossed with *S. campanulata,* although the percentage is so low as to be unreliable. *Sabatia bartramii* and *S. dodecandra* var. *foliosa* crossed infrequently with *S. stellaris.*

Vigorous hybrids resulted from reciprocal crosses of *S. stellaris* and *S. calycina.* There was little variability among the 239 F_1 individuals grown. Hybrids had the large ovary, broad leaves, prominent nodes, and foliose calyx lobes of *S. calycina.* Calyx lobes ordinarily exceeded in length those of the corolla. With *S. stellaris* as the pollen parent, five corolla and calyx lobes characterized the hybrids; when *S. calycina* was the pollen donor six lobes were characteristic. Stained pollen grains often were 4-colpate.

Other hybrids of *S. calycina* with *S. campanulata* and *S. grandiflora* have been grown (Table 3). They clearly incorporated traits of both parents and were largely sterile.

4. CROSSES BETWEEN SECTIONS SABATIA AND PSEUDOCHIRONIA.

Sabatia capitata (Pseudochironia) crossed as the pistillate parent with *S. bartramii* and *S. dodecandra* var. *foliosa*

(Sabatia: Dodecandrae). Only the reciprocal cross with *S. bartramii* as the pistillate parent was occasionally successful.

Sabatia gentianoides (Pseudochronia) crossed with all members of the *Dodecandrae* except *S. calycina*. Only the reciprocal cross using *S. dodecandra* var. *foliosa* as the pistillate parent failed. *Sabatia gentianoides* pollen also effected fertilization in *S. campanulata*, *S. grandiflora*, and *S. stellaris (Sabatia: Campanulatae)*. The reciprocal crosses failed.

Hybrid seed germinability was good. One cross is available for analysis at the present time (Table 3). The hybrids of *S. gentianoides* (♀) × *S. bartramii* were intermediate in vegetative morphology between the parental species. While *S. gentianoides* always has prominent bracts subtending the flowers, the hybrid does not. The number of calyx and corolla lobes was reduced often to 9, but ranged to 12.

SYMPATRY AND ISOLATING BARRIERS

The differentiation of species in *Sabatia* has been accompanied by changes in chromosome number. These changes, which in part reduce or prohibit crossability, are coupled with other isolating barriers. As a result, natural interspecific hybridization is unknown.

A series of 14 extensive field trips during three growing seasons has permitted observations of naturally occurring populations of each species. All sympatric occurrences of species were recorded. As many as five species have been found growing sympatrically, and ten sympatric combinations were noted. In almost every case the species were distributed according to differences in microhabitat. This characteristically non-random distribution was observed in New Jersey by Stone (1908) who wrote: "The curious transition in floras as one approaches the salt water from the pine barrens was beautifully shown about Cold Spring, especially by the *Sabbatias* [sic]. Back at the head of the swamp in a little tract of pine barren affinities, grew the white *S. lanceolata* [= *S. difformis*], which gave way along

TABLE 3

Pollen fertility of F_1 interspecific hybrids in *Sabatia.* The pistillate parent is given first in each hybrid combination.

Hybrid Combination	Percent Stainable Pollen		Grains	Number
	Mean	Range	Scored	Plants
Campanulatae × Campanulatae				
campanulata × grandiflora	44.7	—	1000	1
campanulata × stellaris	8.8	0 - 29.5	1300	6
grandiflora × brevifolia	0	—	300	1
grandiflora × stellaris	0	—	1500	3
stellaris × brevifolia	37.4	—	500	1
stellaris × campanulata	13.5	1.5 - 29.0	1000	4
stellaris × campanulata	56.7	26.0 - 85.0	1200	5
stellaris × "simulata"	26.7	13.5 - 42.0	600	3
stellaris × "simulata"	96.3	88.0 - 99.3	5300	15
"simulata" × stellaris	74.8	37.0 - 95.0	1800	9
Dodecandrae × Dodecandrae				
bartramii × dodecandra var. foliosa	1.6	—	1000	1

(TABLE 3 — *continued*)

dodecandra var. dodecandra × bartramii	0.6	—	1000	1
dodecandra var. foliosa × calycina	10.8	—	1000	1
dodecandra var. foliosa × kennedyana	0	—	anthers aborted	1
Angulares × Dodecandrae				
brachiata × bartramii	0	—	500	1
brachiata × dodecandra var. foliosa	2.6	0 - 7.5	2825	15
dodecandra var. foliosa × angularis	36.6	—	500	1
Campanulatae × Angulares				
campanulata × angularis	52.5	44.7 - 61.6	3000	3
grandiflora × angularis	0	—	5000	4
stellaris × brachiata	1.3	0 - 3.4	1300	4
stellaris × quadrangula	2.6	0 - 5.8	1600	4
Campanulatae × Dodecandrae				
grandiflora × calycina	0	—	800	2
grandiflora × calycina	6.1	0.4 - 23.2	7000	4

stellaris × calycina	0.6	0 - 1.0	1000	3
stellaris × calycina	5.2	0 - 19.0	3000	8
calycina × stellaris	1.9	0 - 5.0	1500	3
Dodecandrae × Difformes				
difformis × kennedyana	0	—	2000	1
kennedyana × difformis	0	—	500	1
kennedyana × macrophylla var. macrophylla	0	—	1000	1
kennedyana × macrophylla var. recurvans	0	—	2000	4
Pseudochironia × Dodecandrae				
gentianoides × bartramii	0.6	0 - 1.2	4000	6

the coastal strip to *S. angularis*, which in turn was replaced by *S. stellaris* in the salt meadows."

The present study reveals that such species found to be sympatric are not intercrossable and belong to different supraspecific categories. Ornduff (1966) has suggested that related species which maintain genetic integrity when sympatric usually are sufficiently distinctive as to be placed in different supraspecific categories by a taxonomist. The only example in *Sabatia* of sympatry involving clearly crossable members of the same subsection was reported by Wilbur (1955). He found mixed herbarium sheets of *S. stellaris* and *S. grandiflora* indicating an overlap in habitats.

Most sympatric species of *Sabatia* differ in floral morphology, and insect visitors vary with the species. In addition, when there is a close aggregation of individuals of a single species, crossing within the population is more likely to occur than is hybridization with another, neighboring species. This massing of flowers of one form tends to discourage indiscriminate pollen transfer by insects into and out of the population (Baker, 1951). Individual species of *Sabatia* frequently are found growing in close stands in favorable situations.

Sabatia brevifolia is seasonally isolated. It flowers from September through mid-November in the southern part of its range. No other related species flowers at that time. *Sabatia kennedyana* is seasonally isolated, for the most part, in North and South Carolina. In New England and Canada it is ecologically and spatially isolated.

Sabatia capitata and *S. arenicola* are spatially isolated from other species in the genus. Strong inherent barriers to crossing exist also.

An inbreeding system further restricts hybridization. Autogamy and correlated morphological adaptations are found in *S. calycina* and *S. arenicola*.

The lack of natural hybrids in *Sabatia* shows the strength of these cytological, ecological, ethological, seasonal, and spatial isolating barriers. In the case of sympatric crossable species, such as *S. grandiflora* and *S. stellaris*, the fact that hybrids are not found in nature is not evidence that

they cannot occur. Rather, their establishment may be prevented by competition. Hybrid seeds of *Sabatia* often are smaller than normal and contain less nutritive tissue. Hybrid weakness is frequent. Even if hybrids were established, gene exchange would be restricted by F_1 sterility barriers.

PATTERNS OF DISTRIBUTION

The majority of *Sabatia* species is found in or restricted to the Coastal Plain, an area which has been available for plant occupancy since early Tertiary time (Core, 1938; Braun, 1964). Lower Tertiary communities contained a relatively high proportion of tropical or subtropical species. By the Eocene, a temperate flora was probably the dominant community in southeastern United States (Graham, 1964). Later events involved expansion of the temperate flora as the Tertiary seas receded, evolutionary development and speciation, and rearrangement of communities during the Pleistocene. It is unlikely that the effect of Pleistocene climatic changes on the southeastern flora was extensive (Graham, l.c.).

Kearney (1900), Fernald (1931), and Core (1938) have postulated that many floristic elements of the southeastern Coastal Plain are derived from an ancestral flora of the Appalachian region. The peneplained Appalachians underwent a series of uplifts during the early Cenozoic Era, with the result that bogs and savanna-like (i.e., hydric and xeric) habitats were eliminated. At the same time the Coastal Plain gradually emerged. Certain Appalachian species migrated to the newly available habitats on the Coastal Plain where the savannas, bogs, shallow pools, and sandy soils provided the environment in which they could survive (Fernald, l.c.).

At present only one species of *Sabatia*, *S. capitata*, is restricted to the southern Appalachians. In the past 100 years its distribution seems to have contracted to a range of mountains in northwestern Georgia and northeastern Alabama. Four other species, *S. angularis*, *S. brachiata*, *S. campanulata*, and *S. quadrangula*, grow in the Appalachian region and elsewhere.

The Ozarkian region has had much the same history as Appalachia. It was isolated from Appalachia during the Tertiary by waters of the Mississippi Embayment (Core, 1938). Ozarkia was proximal to prairie and Sonoran floras on the west, and has floristic affinities with the south and the Appalachian upland (Braun, 1964). *Sabatia campestris* is restricted to Ozarkia and regions to the south and west.

Thus, six species of *Sabatia* occur in one or the other of these refugia, or both *(S. angularis)*. The other species are distributed south and east of Appalachia and Ozarkia in the Piedmont and Coastal Plain.

Sabatia stellaris (including "*S. simulata*") occurs in Mexico as well as in eastern United States, the Bahamas, and Cuba. It likely had a wider distribution in the past and has now disappeared from Texas, where there are seemingly suitable habitats, leaving disjunct stands in Mexico. Dressler (1954) remarked that such Mexican-eastern U.S. disjunct species invaded Mexico in response to environmental stress during the Pleistocene. Rather than zonal displacement, glaciation may have caused regional extinction and disruption of the range (Webster, 1970).

Also, *S. kennedyana* may have had a wider distribution at one time. It is presently known from northeastern South Carolina, southeastern North Carolina, Rhode Island, eastern Massachusetts, and Nova Scotia. *Scirpus longii* Fern. has a similar distribution. Fernald (1943) suggested that this species and others with comparable distributions migrated along the once emergent continental shelf and were isolated when the shelf became submerged.

The varieties of *S. macrophylla* are separated in Georgia by no more than 50 miles, but in Florida they are absent in the area between Tallahassee and Lake City. Ward (1967) said, "The absence of an otherwise widespread species in the area between Leon and Columbia counties is a frequent feature of plant and animal distribution in Florida." Repeated atempts to locate *S. macrophylla* in this region have been unsuccessful. As Ward noted, the area was occupied by an embayment of the Gulf of Mexico during Pleistocene interglacial periods (MacNeil, 1950). At times of greatest

inundation the embayment isolated peninsular Florida and extended across southeastern Georgia (Ward, l.c.). Probably as a result the populations of *S. macrophylla* were isolated from one another and became weakly differentiated. The closely related *S. difformis* has a similar gap in Floridean distribution, but populations are not morphologically discontinuous. The fact that other species *(S. bartramii, S. campanulata, S. gentianoides)* are also absent between Leon and Columbia counties suggests microenvironmental unsuitability.

The remaining species of *Sabatia* have rather conventional Coastal Plain patterns of distribution. The species probably arose from one or more ancestral taxa which existed in the Appalachian refugium in Tertiary times or before. They possibly evolved in the Appalachian highlands and migrated to the Coastal Plain or, alternatively, evolved in the Coastal Plain from earlier migrants.

TAXONOMIC RELATIONSHIPS

As with almost all species, those of *Sabatia* were originally recognized by morphological discontinuities. The experimental data presented here leave no doubt that the species *per se* are discrete phyletic units having chromosomal and genetic differences. However, arrangement of species in the systematic hierarchy followed heretofore and recognition of varieties are subject to re-examination.

Section Sabatia

Subsect. Difformes. This subsection is maintained without change. The species (*S. difformis* and *S. macrophylla*) are perennials and closely related; crossability barriers are not stringent. Fertility of hybrids is unknown. The species cross rather freely with members of two other subsections, *S. quadrangula (Angulares)* and *S. brevifolia (Campanulatae)*. It may not be coincidental that these four species are exclusively white-flowered. All other species in the genus are basically pink-flowered. Blake (1915) placed *S. difformis* and *S. macrophylla* with *S. quadrangula* (as *S. paniculata*) in his subsection *Angulares*. *Sabatia brevifolia* has never been allied with these.

If the hybrids from crosses of *S. quadrangula* and members of *Difformes* are fertile, *S. quadrangula* should be allied with subsect. *Difformes.* Gleason (1952) noted that *S. quadrangula* is "very close to *S. difformis* in describable characters . . ." However, *S. quadrangula* and *S. brevifolia* have crossing and stronger morphological affinities with other species as well. For that reason they are not at present considered to belong to subsect. *Difformes.*

The two varieties of *S. macrophylla*, var. *macrophylla* and var. *recurvans*, are maintained. They have distinct geographical ranges and there is no evidence that they intergrade in nature or occur in the same population. They may be distinguished readily by the recurvation and length of colyx lobes. These differences are retained by cultivated plants grown under uniform conditions. Specific status (*cf.* Small, 1933) is not justifiable in view of their close morphological, cytological, and crossability relationship.

Subsect. ANGULARES. Members of *Angulares* do not have strong crossing affinities, but they are morphologically related and are biennials. *Sabatia angularis* and *S. quadrangula* (characterized in part by pink and by white corolla lobes, respectively) are closely related morphologically; but they are strongly differentiated in terms of crossability and chromosome number. *Sabatia brachiata* (with pink corolla lobes) is more remote from *S. angularis* in both morphology and chromosome number. The similarity in chromosome numbers does not justify reconsideration of taxonomic rank for *S. brachiata* and *S. quadrangula.* The two are readily distinguished morphologically. The cytological races of *S. quadrangula* are not phenotypically differentiated and are not given taxonomic recognition.

Members of *Angulares* seem to have a transitional crossing relationship with the other subsections as here delimited. *Sabatia brachiata* crosses with members of *Campanulatae* and *Dodecandrae. Sabatia quadrangula,* in addition to crossing with *Difformes*, produces sterile hybrids in crosses with *S. stellaris (Campanulatae). Sabatia angularis* crosses with *Campanulatae* members and with *S. dodecandra* var. *foliosa (Dodecandrae).* Thus, no clear pattern emerges

which would justify allying these species with those of other subsections. Members of *Angulares* may be nearest among extant species to the ancestral stock of *Sabatia* since they bridge the gap between annuals and perennials as far as crosses are concerned.

Subsect. CAMPANULATAE. In the *Campanulatae* all species except *S. brevifolia* are intercrossable, and certain hybrids are partially fertile. Seeds are produced by crosses involving *S. brevifolia,* but they are small and the seedlings are weak. Nonetheless, crossability in certain directions is high. On these and morphological grounds *S. brevifolia* is kept in subsect. *Campanulatae.*

The other three species traditionally placed in *Campanulatae* are intercrossable and more closely related to each other than to *S. brevifolia.* Wilbur (1955) considered *S. grandiflora* ($n=18$) closer to *S. stellaris* ($n=18$) than to *S. campanulata* ($n=17$). This conclusion is supported by chromosome numbers and crossability relations. However, hybrids from the cross *S. grandiflora* (♀) × *S. stellaris* are sterile whereas those involving *S. stellaris* and *S. campanulata* are semi-fertile. In the latter crosses the partial sterility is probably due to imbalance resulting from differences in chromosome number of the parental species. The sterility of hybrids from *S. grandiflora* × *S. stellaris* may be more fundamental, resulting from disharmonies between the genomes differing genetically or structurally. It is apparent that crossability and hybrid fertility are not correlated positively in all instances.

Gleason (1952) remarked that *S. stellaris* ". . . and *S. campanulata* constitute the local extremes of a variable population which may represent only one species or as many as four," the others being *S. brevifolia* and *S. gracilis* (Michx.) Salisb. Wilbur (1955) reduced *S. gracilis* to synonymy with *S. campanulata,* and this decision is supported by my field and greenhouse observations. Greenhouse progeny of the "*gracilis*" type take on the typical growth form of *S. campanulata* (*see* synopsis of taxa) and chromosome numbers are similar ($n=17$). *Sabatia campanulata* is perennial; the other two species are annual, and

all three differ in chromosome number, crossability, and morphology. They cannot be considered a single variable population.

Britton (1905) and Britton and Millspaugh (1920) recognized two species of *Sabatia* as growing in the Bahamas, "*S. campanulata*" and the supposed endemic "*S. simulata.*" The latter species was distinguished from pink-flowered "*S. campanulata*" by its smaller, white flowers and more slender habit (*see* synopsis of taxa). Wilbur (1955) referred "*S. simulata*" and the pink-flowered Bahamian populations to *S. stellaris.* Collections of *Sabatia* from islands of Abaco, Eleuthera, Grand Bahama, and New Providence were made for this study. Chromosome numbers of the color phases are the same as *S. stellaris* and no combination of characters adequately delimits all Bahamian specimens from the mainland *S. stellaris.*

Reduced crossability of the Bahamian taxon and mainland *S. stellaris* suggests that genetic changes have accumulated in the spatially isolated populations. Most of the crosses reported here involved plants from New Providence Island. Average pollen fertility of the hybrids was somewhat lower than that of the parental species (Table 3). But the values include viability estimates made early in the flowering season. Subsequent estimates were much higher and indicate that there is no substantial reduction in hybrid fertility. As Wilbur noted, formal taxonomic recognition of the Bahamian populations is not justified. All are referable to *S. stellaris.*

Plants from the Abaco "whitelands" do seem to have stronger barriers to crossing with *S. stellaris*; plants are more distinctive morphologically than are those from New Providence. The Bahamian populations of *S. stellaris* constitute geographical races which are gradually diverging genetically from the mainland populations.

Sabatia calycina is transferred from subsect. *Dodecandrae* to *Campanulatae.* Blake (1915) placed it with pentapetalous species in *Campanulatae*; the species was transferred to subsect. *Dodecandrae* by Wilbur (1955). Morphological evidence is subject to either interpretation.

Cytological evidence has not resolved the dispute over placement of *S. calycina,* but its crossing relationships are clearly with members of the *Campanulatae.* There is no evidence that it crosses readily with members of *Dodecandrae.*

Sabatia calycina is a polyploid (n=32). Its regular meiosis with no evidence of multivalents suggests it is a balanced allopolyploid. As yet there is no information with regard to its origin.

Subsect. DODECANDRAE. Members of *Dodecandrae,* with *S. calycina* excluded, show strong crossability with one another. They are polypetalous and perennial.

Ahles (1964) reduced *S. kennedyana* (n=20) and (as var. *coriacea*) *S. bartramii* (n=18) to varietal rank under *S. dodecandra* (n=17). He placed *S. harperi* Small, a synonym of *S. foliosa* Fern. (= *S. dodecandra* var. *foliosa*; n=19), in the synonymy of *S. dodecandra* var. *dodecandra.* The transfer of rank was effected by citing the basionym, and no justification was presented for the change. Though the taxa are intercrossable, they differ in chromosome number; fertility of artificial hybrids, where known, is low (pollen viability 1.6% or less). *Sabatia bartramii* and *S. dodecandra* var. *foliosa* are largely sympatric but natural hybrids do not occur. *Sabatia dodecandra s. s.* and *S. kennedyana* are distinctive ecologically and geographically. The morphological features separating these taxa are as strong as characters distinguishing members of other subsections. There is no justification for recognizing *S. kennedyana* and *S. bartramii* as varieties (*see* Wilbur, 1970, for further discussion).

Wilbur (1955) reduced *S. foliosa* (n=19) to varietal rank under *S. dodecandra* (n=17 + 2 pairs accessory chromosomes). If the cytological difference proves to be stable throughout the respective ranges and if hybrids are sterile, a reconsideration of specific rank should be undertaken (*see* Wilbur, 1970); additional work is in progress. The taxa are strongly dissimilar ecologically and occupy distinctive geographical ranges.

Section PSEUDOCHIRONIA

The two members of *Pseudochironia* were at one time segregated in a separate genus, *Lapithea* (Grisebach, 1845; Small, 1903, 1933). There are morphological differences of a higher order of magnitude between members of sect. *Pseudochironia* and subsect. *Dodecandrae* than within *Dodecandrae*. However, sect. *Pseudochironia* does not have the reproductive isolation of sect. *Campestria*, to follow. *Sabatia gentianoides* ($n=14$), as noted previously, crossed with members of subsect. *Dodecandrae* (sect. *Sabatia*). *Sabatia capitata* ($n=38$) crossed with *S. dodecandra* var. *foliosa* ($n=19$) and with *S. bartramii* ($n=18$). Sectional rank best expresses the morphological discontinuities while generic rank obscures the obvious phylogenetic relationship to subsect. *Dodecandrae*.

Sabatia capitata is believed to be a relict amphiploid. The relationship of *S. capitata* and *S. gentianoides* is unclear. *Sabatia capitata* is probably more primitive than the Coastal Plain *S. gentianoides* which has reduced and modified foliage (Wilbur, 1955). The two have widely diverse chromosome numbers and are not intercrossable. They may be related through a common ancestor from which *S. gentianoides* has evolved by a chromosomal reduction series.

Section CAMPESTRIA *stat. nov.*

Subsect. *Campestres* Blake, Rhodora **17**: 65. 1915.
Neurola Raf., New Fl. **4**: 92. 1838.

The *Campestres* group is worthy of sectional rank. *Sabatia campestris* ($n=13$) and *S. arenicola* ($n=14$) seem to represent a now well differentiated line of evolution in the genus. They are genetically isolated from other members of the genus and for the most part they are geographically isolated as well. Only *S. angularis* and *S. campestris* overlap in distributions. The chromosome numbers are the lowest in the genus with the exception of *S. gentianoides* ($n=14$) which is not closely related either morphologically or genetically. This evidence, when combined with that of morphology, suggests a greater evolutionary hiatus between these species and members of sect. *Sabatia* than is implied when *Campestres* is placed in sect. *Sabatia*.

Considering its present distribution, the outbreeding *S. campestris* may have originated from an Ozarkian ancestor. On morphological grounds, the inbreeding *S. arenicola* is closely related, although the two are genetically isolated from each other. *Sabatia arenicola* probably originated as a self-pollinating race from an ancestral outcrossing race. In view of its present littoral habitats in Texas and Mexico, catastrophic selection for early maturing genotypes may have occurred (cf. Lewis, 1962).

Although *S. arenicola* now grows only on recent (Quaternary) land deposits, there were earlier shore lines on which it could have evolved. There is, therefore, no reason to assume a recent origin for the species. Its lack of crossability with *S. campestris* supports this assumption.

Section *Campestria* is most closely related to subsect. *Angulares.* Species in both groups have quadrate stems margined at the angles by a thin membrane, together with other characteristics in common (*see* Wilbur, 1955).

Sabatia is usually placed near *Centaurium* Hill in taxonomic treatments of the family. The relationship is closest through sect. *Campestria* whose members extend into the easternmost range of *Centaurium. Sabatia arenicola* bears a striking, if perhaps superficial, resemblance to certain Centauriums. This line of evolution may be interrelated with that of *Centaurium.*

DISCUSSION

The hybridization program has been most useful in testing the validity of taxonomic groupings and in elucidating patterns of relationship. In general, views of discontinuity denoted by the supraspecific divisions of Wilbur (1955) are supported by these data. There are several species (*S. brachiata, S. brevifolia, S. calycina, S. gentianoides,* and *S. quadrangula*) which show greater inter(sub)sectional than intra(sub)sectional crossability. Certain ones of these partially bridge morphological and cytological gaps between the subsections or sections involved. They may represent steps in evolutionary series of anastomoses in a phylogenetic web (*cf.* Levin, 1966).

The occurrence of unequal viable seed set in reciprocal crosses has been reported in recent papers by Mason (1952; *Limnanthes*), Grant (1956b; *Gilia*), Vickery (1959; *Mimulus*), Vasek (1964; *Clarkia*), Ellison (1964; *Bahia*), and Levin (1966; *Phlox*). Reciprocal differences often are correlated with differences in style length or with cytological abnormalities or sterility factors. None of these accounts for unequal reciprocal crossability in *Sabatia*. Analysis of *Sabatia* crosses shows that, in addition to unequal seed set, dissimilar hybrids may result from reciprocal crosses.

There may be in *Sabatia* a cytoplasmic or maternal influence on morphology and seed formation similar to that noted in *Gilia* (Grant, 1956b). Since most of the crosses have been heteroploid, there are ploidal influences as well. In this study 51 reciprocal heteroploid crosses had unequal seed set. Of these, 37 or 73% had a higher seed set when the pollen parent was of lesser ploidy than the pistillate parent.

The difference in chromosome number is in itself a barrier to formation of fertile hybrids in *Sabatia*. This barrier does not necessarily operate at the level of initial crossability. While heteroploid crosses do not give a true indication of genetic relationship, they show that aneuploidy has been an effective source of karyological variation leading to reproductive isolation among closely related species and, presumably, to species formation.

Basic chromosome numbers known in the Gentianaceae are x = 5, 6, 7, 8, 9, 11, 12, 13, 15, and 17 (Löve, 1953; Darlington and Wylie, 1955; Khoshoo and Tandon, 1963). Numbers of x = 5, 7, 9, and 13 seem to be, in occurrence, the principal basic numbers. Chromosome numbers are known for about 130 species belonging to 20 genera (Khoshoo and Tandon, l.c.), approximately 19% of the total species (700) in the family.

The number x = 13 has been explained in different ways. Favarger (1949) suggested that the number 13 was derived from x = 7 through polyploidy followed by fusion of two chromosomes. He assumed that the original number of the family was x = 5 and that the higher number of

x = 11 was derived through polyploidy followed by fragmentation.

Skalinska (1952; reviewed in Löve, 1953) found a basic number of x = 6. According to Löve (l.c.) and Khoshoo and Tandon (1963), the numbers 11 and 13 more likely are secondary basic numbers which have been compounded from 5 + 6 and 6 + 7 respectively. Thus, the numbers 5, 6, and 7 are primary basic numbers in the family.

In *Sabatia* the basic number could be 7. By remote and now concealed polyploidy (Darlington, 1956) tetraploids and hexaploids may have arisen. Through these the array of chromosome numbers now known for contemporary species could have been derived by aneuploid reduction and secondary polyploidy.

The wide variation in basic chromosome numbers of Gentianaceae shows that generic diversification has been based largely on alloploidy (Löve, 1953). In her opinion evolution at the species level has been based on formation of abrupt-species by polyploidy and on gradual evolution of species with identical chromosome numbers. To these may be added aneuploidy in *Sabatia* and in *Swertia* (Khoshoo and Tandon, 1963). The two polyploids in *Sabatia* support the argument of Rork (1949) that, in Gentianaceae, polyploids have neither a wider distribution nor a more northern distribution than that of diploids.

The experimental data presented here strengthen impressions of morphological discontinuity among species of *Sabatia*; reproductive discontinuities are strictly correlated with those phenotypic characteristics which differentiate species. There is no hybridization in nature although an outcrossing system prevails and vigorous hybrids can be obtained artificially with some facility. External barriers to hybridization include ethological, seasonal, spatial, and ecological isolation. While internal crossability barriers are stronger among sympatric species than among allopatric ones, sterility barriers to back-crossing or formation of advanced generation hybrids are generally stringent in either case. The occurrence of natural polyploidy and of strong crossability or sterility barriers, together with its lack of

cytological uniformity, indicate that *Sabatia* is a genus at an advanced stage of evolution and of considerable age.

ACKNOWLEDGMENTS

I thank the following persons who collected live plants or cytological material of *Sabatia*: Sylvia A. Earle, P. F.-C. Greear, Olga Lakela, R. W. Long, Barbara M. Grigg, D. E. Stone, and R. L. Wilbur. Dr. J. W. Berry identified the flower spiders.

Although this study was not based upon herbarium specimens, I have examined a number of collections. For this courtesy I wish to thank curators of the following herbaria: DUKE, FLAS, FSU, GA, NCU, NSC, TENN, US, and USF.

The guidance of Drs. Donald E. Stone and Robert L. Wilbur is gratefully appreciated.

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THE SYSTEMATICS AND ECOLOGY OF POISON-IVY AND THE POISON-OAKS (TOXICODENDRON, ANACARDIACEAE)

WILLIAM T. GILLIS

(Continued from page 237)

4g. **Toxicodendron radicans** subsp. **divaricatum** (Greene) Gillis, stat. nov. Fig. 44.

Toxicodendron divaricatum Greene, Leafl. Bot. Observ. Crit. 1: 122. 1905. *Rhus divaricata* (Greene) McNair, Publ. Field Mus. Nat. Hist. 225, Vol. 4: 69. 1925, non Eckl. and Zeyh., Enum. Pl. Afr., p. 146. 1834. *Rhus greenei* McNair *(ibid.)*, insert after page 69. *Toxicodendron radicans* var. *divaricatum* (Greene) Barkley (as *divaricata*), Ann. Missouri Bot. Gard. 24: 433. 1937. *Rhus radicans* var. *divaricata* (Greene) Fernald, Rhodora 43: 596. 1941. Type: *Purpus*, s.n., Mexico, Calmalli, Baja California Norte, 700-900 feet. Jan.-Mar. 1898. (US-383431, lectotype of Barkley, 1937).

Rhus tridentatum Sessé and Moçiño, Pl. Nov. Hisp., p. 47. 1887. non Thunb. ex L.f. Suppl. 184. 1781, nec Sond. ex Harv. and Sond., Fl. Cap. 1: 511. 1859, nec Willd. ex Engler in DC., Monogr. Phanerog. 4: 438. 1883. *Rhus saxatilis* DC. Prodr. 71. 1825. Type: "Habitat in calidis Nouae Hispaniae regionibus, et capite Bonae Spei. Floret uere." (MA, lectotype; F-1572884, photograph of type).

Toxicodendron laetevirens Greene, Leafl. Bot. Observ. Crit. 1: 123. 1905. *Rhus radicans var. laetevirens* (Greene) Fernald, Rhodora 43: 596. 1941. Type: *J. W. Toumey*, s.n. Arizona, Pima Co., Santa Catalina Mts., 5 May 1894. (US-441725, holotype; A, GH, NY (3 specimens), US-619140, isotypes; MO-144536, photograph of type).

Toxicodendron phaseoloides Greene, Leafl. Bot. Observ. Crit. 1: 123. 1905. Type: *C. V. Hartman* 102. Mexico, Sonora, Turicachi, 5600 feet altitude, 7 Dec. 1890. (US-306157, holotype; GH, NY, isotypes).

Toxicodendron arizonicum Greene, Leafl. Bot. Observ. Crit. 1: 123. 1905. Type: *Edward Palmer* 453a, Arizona,

Fig. 44. *Toxicodendron radicans* ssp. *divaricatum*. Holotype of *Toxicodendron arizonicum* Greene, *Palmer*.

Cochise Co., Fort Huachuca, 26 April-21 May 1890. (US-19847, holotype; GH, NY, isotypes; MO-144549, photograph of type).

Vine or shrub. Leaflets entire, subentire, or occasionally notched, elliptic, lanceolate, or ovate, glabrous, rarely strigose on the lower surface or with sparse pubescence confined to the primary veins, not velvety to the touch; upper leaflet surface glabrous, not lustrous, usually decidedly darker than the lower surface; veins light-colored, prominent on both surfaces. Leaflets usually 1.9-3 times as long as broad with larger leaves southward in the range; petiole 1.5-12.0 cm long, scattered to densely puberulent; terminal blade 1.5-16.0 cm long, 0.6-9.0 cm wide; terminal petiolule 0.2-6.0 cm long; lateral leaflets often as long or longer than terminal. Tip acuminate, usually long tapering; base subcuneate; lower surface with occasional tufts of strigose hairs in the major vein axils, disappearing completely in the southern end of the range. Fruit globose, glabrous (glabrate in the northern end of the range), 3.0-6.0 mm broad, larger southward than in the north. Flowering March to June.

Distribution: Mexico and United States: Sierra Madre Occidental, north to southeastern corner of Arizona. (Fig. 41.)

Representative specimens: UNITED STATES. **Arizona.** COCHISE CO.: Fort Huachuca, *Palmer* 453a (GH, MO, NY, US); Bisbee, *Goodding* 46 (ARIZ); one mile above Paradise, *Blumer* 98a (US); Huachuca Game Reserve, *Goodding* 1104-49 (ARIZ); Chiracahua National Monument, *Clark* 8095 (ARIZ). PIMA CO.: Santa Catalina Mts., *Toumey*, s.n. (A, ARIZ, GH, MO, NY, US); Santa Catalina Mts., Upper Bear Canyon, *Gillis* 6687 (MSC); Santa Catalina Mts., Sabino Canyon, *Rehder* 480 (A), *Jones*, s.n. (RM), *Toumey* 139 (US); Fort Lowell, *Lemmon*, s.n. (MO); Morista Canyon, Baboquivari Mts., *Clark* 11638 (GH); Florida Canyon, Santa Rita Mts., *Graham*, s.n. (NY). SANTA CRUZ CO.: Santa Rita Mts., Sycamore Canyon, *Henly, Mason, & Stokes* 2257 (ARIZ); Stone Cabin Canyon, *Thornber & Griffiths* 139 (ARIZ); Santa Rita Forest Preserve near Amado, *Griffiths* 4222 (MO); vicinity of Nogales, *Rose* 11943 (US); 2.95 miles SW of Patagonia, *Gillis* 6716 (ARIZ, MSC).

MEXICO. **Aguascalientes:** Road to Calvillo, 21 miles west of Aguascalientes, *McVaugh & Koelz* 158 (MICH). **Baja California:**

Calmalli, *Purpus*, s.n. (US). El Chorro, *Moran* 7307 (GH). LaLaguna, *Moran* 7431 (ARIZ, GH). **Chiapas:** Paraje of Mahosik, Municipio of Tenejapa, *Breedlove* 14890 (DS, MSC); Pokolom, paraje of Sibanikha, Municipio of Tenejapa, *Breedlove* 11736 (DS). **Chihuahua:** St. Diego, *Hartman* 589 (F, GH, NY, US). Guadeloupe Canyon, *Mearns* 579 (US). Carretos, border of Chihuahua and Sonora, Municipio de Janos, *White* 2551 (GH, MICH, TEX). Loreto near Rio Mayo, *Gentry* 2857 (A, ARIZ, MO). Cajon Creek near US boundary line, *Mearns* 394 (GH, MO, US). **Coahuila:** Sierra de la Gloria, southeast of Monclova, *Marsh* 1973 (F, GH), *Parras, Aguirre & Reko*, s.n. (NY). **Durango:** Cerro Chupadero, 45 miles south of El Salto, west of Pueblo Nuevo, *Maysilles* 8211 (MICH). Pueblo Nuevo, *Baker*, s.n. (MSC). Durango, *Palmer* 106 (F). **Guanajuato:** locality unknown, *Dugès* 483 (GH, US). **Hidalgo:** Ixmiquilpan, *Rose, Painer, & Rose* 8950 (NY, US). Barranco de Toliman below Mina Loma de Toro, *Moore* 2599 (GH). **Jalisco:** Sierra del Nayarit, *Diquet*, s.n. (NY). Zahotlan, *Pringle*, s.n.(TEX). Sierra del Halo, *DeJong* 1043 (MSC). Mazamitla, *Donahue* 16 (MSC). Zapotlán, *Salizar*, s.n. (TEX). Vicinity of San Juan Cosalá, north of Lake Chapala, *Puga*, s.n. (MICH). Barrancas of Rio Verde, 20 miles north of Tepatitlán, road to Yahualica, *McVaugh* 17426 (MICH). Ravine bottom in mountains east of Mamantlán, 15 miles SSE of Autlán, *Wilbur & Wilbur* 2074 (MICH). Forested crest of ridge facing Pacific, 10 miles south of Autlán, *Wilbur & Wilbur* (MICH). Summit of volcanic cliffs 8 miles SE of Jalostotitlán, road to San Miquel el Alto, *McVaugh* 17553 (MICH). North slopes Nevado de Colima, near jct. of pack road to Zapotlán, *McVaugh* 14934 (MICH). Sierra del Digre, 3 miles south of Mazamitla, *McVaugh* 13606 (MICH). **México:** Locality unknown, *Sessé & Moçiño* 930 (MA). **Michoacán:** Zitacuaro, *Hinton* 13151 (MICH, NY). Mt. Patamban, *Nelson* 6572 (GH, NY, US). Morelia, Loma St. Maria, *Arsène* 2763 (A, GH, MO, US); Morelia, *Arsène* 3011 (A, ILL, MO, NY, US). Apatzingan, Tancitaro Region, Las Barranquillas, *Leavenworth & Hoagstrall* 1817 (F, ILL). Patzcuaro, *DeJong & Longpre* 1081 (MSC). NE of Puentacillas, north of Ario de Rosales, *Iltis, Koeppen, & Iltis* 865 (WIS). Lava flow east of San Juan Nuevo, 8 miles south of Uruapán, *King & Soderstrom* 4750 (MICH). **Nuevo León:** Hacienda Vista Hermosa, south of Monterrey, *White* 1543 (ARIZ, GH, MICH). Mountains 7 miles east of Iturbide, *McVaugh* 10576 (MICH). **Oaxaca:** Oaxaca Courts motel in Oaxaca, *Beaman* 3660 (MSC). Tamazulapam, *DeJong* 1402 (MSC, MU). **Queretero:** Tequisquiapan, *Nelson* 3878 (GH). **San Luis Potosi:** 2 km. SE Ahuacatlán, Xilitla, *Rzedowski* 10970 (MICH). Tolentino, *Meavry* 7373 (TEX), between San Luis Potosí and Rio Verde, *DeJong* 1571 (MSC, MU). Between Ciudad del Maiz and El Naranjo, *DeJong* 1579 (MSC, MU). El Naranjo, *Donahue* 26 (MSC). **Sinaloa:** Bufa de Surutato, Ocurahui, *Gentry* 6389 (ARIZ, GH, MO, NY, US). East of Mazatlán, *DeJong* 1705 (MSC, MU). **Sonora:** Turicachi, *Hartman* 102 (GH, NY, US). Rancho de la Nacha, *White* 3990 (ARIZ, GH,

MICH, US). Junction of roads to Cananea and Remedios on Rio Magdalena, *Wiggins* 7099 (A, ARIZ, DS, MICH, US). Canyon de los Apaches, north of Aribabi, *White* 2763 (GH, MICH). Region of Cordova, *Borgeau* 2257 (GH). El Rancho del Roble, northeast of El Tigre, *White* 4238 (ARIZ, GH, MICH). Bacoachio near Esqueda, *Wiggins* 11716 (US). Alamo, Mt. Magdalena, *Kennedy* 7106 (US). Canyon of Guadeloupe River, *Smith*, s.n. (NY). Sabino Canyon, Quirocoba, Rio Fuerte, *Gentry* 2246 (A, ARIZ, F, MO, TEX, US). San José Mountains, *Mearns* 1052 (US). Santa Rosa Canyon, near Bavispe, *White* 497 (ARIZ, MICH, GH), Canon International, *White* 3505 (GH, MICH). Sierra Madre Occidental, Sierra Charuca, Canon de Tejas, *Gentry* 6389 (ARIZ, MICH). TAMAULIPAS. Dulces Nombres and east into Tamaulipas, *Meyer & Rogers* 2809 (MO).

Barkley (1937) separated this taxon from others on the basis of a constriction at the side of the seed, a feature often difficult to interpret if it does, indeed, exist. Even the divaricate nature of the inflorescence, which gives the taxon its name, is difficult to see as unique to this plant. When McNair transferred this taxon to *Rhus*, he neglected the Ecklon and Zeyher South African species of that name; so he had a correction slip bound into his article before distribution, changing the name to *Rhus greenei*. So far as I can determine, this name was never affixed to a single specimen.

In citing specimens in connection with *Toxicodendron phaseoloides*, Greene did not designate one of the specimens he saw as type. Barkley *(ibid.)* chose *Hartman* 102. Greene describes his material as having "abruptly acuminate" leaflets, but they are not. Likewise, in his diagnosis of *T. laetevirens*, Greene indicated that the foliage was light green. The type has apparently no brighter green leaves than Greene's twelve other poison-ivy species. Presumably the collections were already dried when Greene affixed names to them, since he was not the collector; therefore, they probably appear today much the same as they did to him.

According to Engler (in DeCandolle, 1883), *Rhus saxatilis* DC. (1825) is a doubtful species and is probably not anacardiaceous. No specimen is known to represent this species in the DeCandolle Herbarium. We would have no idea of what DeCandolle had in mind except for a later

reference to the plant (DeCandolle, 1874). *Rhus saxatilis* was based on one of the Sessé and Moçiño paintings (cited as pl. 192 in the Calques des Dessins, DeCandolle, 1874). This is the same plate that was cited as Ic. Fl. Mex. 196 under *Rhus tridentatum* by Sessé and Moçiño (1887). Since there is a type specimen for the Sessé and Moçiño binomial, we can equate the dubious *R. saxatilis* with a given specimen which is *Toxicodendron radicans* subsp. *divaricatum*. According to Dr. Rogers McVaugh (personal communication), the type locality was in Morelos (Yacapixtla and Cuernavaca).

This taxon flowers from March to June, but chiefly in late April and early May, as distinguished from subsp. *barkleyi*, which flowers from May to August, chiefly in June and early July. Although intergrades between these two subspecies are known, it is likely that their different flowering periods act as a barrier to gene exchange in the regions where their ranges overlap.

Subspecies *divaricatum* is found in southeastern Arizona and western Mexico: the Sierra Madre Occidental and the western portion of the trans-Mexico volcanic belt. It is in this central region of Mexico wherein intergrades, presumed hybrids, have been found between subsp. *divaricatum* and *barkleyi*.

This subspecies is found at moderate elevations, but often is restricted to heavily wooded canyons or south-facing slopes intermixed with tussock grasses. On the one occasion I have had to study it in the field, it was found in moist canyons near creeks or springs. The species of trees making up the dominant vegetation in this locality in southeastern Arizona were *Salix laevigata*, *Fraxinus pennsylvanica* subsp. *velutina*, *Cupressus arizonica*, *Pinus cembroides*, and *Juglans major*. Other species were shrubs such as *Rhus trilobata*, *Rhamnus californica*, *Prunus emarginata*, and *Ceanothus fendleri*. The associated herbs were mostly weeds.

The taxon probably has its closest affinities with subsp. *verrucosum*. The latter subspecies may have been derived from subsp. *divaricatum* after it was isolated from it as a separate population.

Fig. 45. *Toxicodendron radicans* ssp. *verrucosum*. Holotype of *Rhus rhomboidea* Small, *Heller* 1670.

Fig. 46. *Toxicodendron radicans* ssp. *verrucosum*. Left: Lectotype of *Rhus verrucosa* Scheele, *Lindheimer* 401. (Right: *Toxicodendron radicans* ssp. *pubens*, *Lindheimer* 346. These specimens formerly were mounted on the same sheet, see discussion in the text.)

4h. **Toxicodendron radicans** subsp. **verrucosum** (Scheele) Gillis, comb. nov. Figs. 45, 46

Rhus verrucosa Scheele, Linnaea 21: 592. 1848. *Toxicodendron verrucosum* (Scheele) Greene, Leafl. Bot. Observ. Crit. 1: 124. 1905. *Toxicodendron radicans* var. *verrucosum* (Scheele) Barkley, Ann. Missouri Bot. Gard. 24: 435. 1937. (as *verrucosa*). *Rhus radicans* var. *verrucosa* (Scheele) Fernald, Rhodora 43: 596. 1941. Type: *F. Lindheimer* 401. In Hecken auf felsigem Boden auf dem Missionshugel bei Neubraunfels; Lindheimer. May 1845. (GH, lectotype; MO-1774754, isotype).

Rhus rhomboidea Small, Fl. S.E.U.S., 727. 1903. *Toxicodendron rhomboidea* (Small) Greene, Leafl. Bot. Observ. Crit. 1: 125. 1905. Type: *A. Arthur Heller* 1670. (NY, holotype; E, F-171075, MIN-149968, MO-1774757, MSC-53804, US-213781, isotypes).

Vine or shrub with aerial roots; leaflets rhomboid-ovate, acute to acuminate, usually regularly and deeply incised dentate or acute-angled lobed, glabrous (rarely strigose) above, occasionally with a line of minute curly hairs on the midrib above; glabrous to substrigose below, with hairs confined to the primary and secondary veins, rarely with tufts of hairs in the vein axils; leaflet blade tip sharply acute, base cuneate or obtuse. Petiole glabrous to pilose, rarely short tomentose, 3.2-11.0 cm long; terminal leaflet blade 3-13 cm long, 2-11 cm wide, terminal petiolule 0.5-4.0 cm long. Fruit glabrous 2.5-5.5 mm broad.

Distribution: Texas and Oklahoma: Edwards Plateau and Arbuckle Mts. on limestone. (Fig. 39.)

Representative specimens: UNITED STATES. **Texas.** BASTROP CO.: Beuscher State Park, *Gillis* 3750 (MSC); Bastrop State Park pine hills, *Duval*, s.n. (TEX); *Gillis* 5161 (MSC). BEXAR CO., Leon Springs *Clemons & Clemons* 830 (RM). COMAL CO.: New Braunfels, *Lindheimer* num. plur. (GH, KSC, MIN, MO, US). CORYELL CO.: 5.6 miles east of Gatesville, *Shinners* 28292 (FSU, SMU). DALLAS CO.: Dallas, Northwest Highway, *Gillis* 5149 (MSC). GILLESPIE CO.: locality unknown, *Jermy*, s.n. (MO). GRAYSON CO.: Denison, *Kohfeldt* 33 (TEX). HARRIS CO.: Houston, *collector unknown* (MO). HARRISON CO.: Marshall, *Gillis* 3772 (MSC). HILL CO.: Hillsboro, *Gillis* 5153 (MSC). KERR CO.: Kerrville, *Heller*, 1670 (ARIZ, E, F, GH, MIN, MO, MSC, NY, US); Turtle Creek, *Bray* 189 (TEX). MEDINA CO.: Castroville, shore of Rio Medina, *Gillis* 5183 (MSC). MENARD CO.: Menard, *Palmer* 11898 (RM). REAL CO.: locality unknown, *Boyles*, s.n. (TEX). Tarrant, Lake Como, *Ruth* 941 (MSC, NY); ravine near Trinity River, *Ruth* 7530 (PH). TOM GREEN CO.: Dove Creek, *Tweedy* 133 (US). TRAVIS CO.: Austin, *Gillis* 3679 (MSC); Bergstrom Air Force Base, *Gillis* 5154 (MSC); Barton Springs, *Krodel* 32 (TEX). UPSHUR CO.: Gladewater, *Gillis* 3766 (MSC). UVALDE CO.: Uvalde along wooded banks of Leana River, *Palmer* 33630 (PH); Uvalde along Frio River, *Gillis* 5193 (MSC). WOOD CO.: Hawkins, *Gillis* 3769 (MSC). LOCALITIES UNCERTAIN: 18 miles SW of View on Edwards Plateau, *Tolstead* 7563 (TEX). Columbia, *Bush* 142 (A). **Oklahoma.** LOVE CO.: Hickory Creek, *Gillis* 5148

(MSC). MURRAY CO.: Turner Falls, *Gillis* 5142, 5137 (MSC). WOODS CO.: locality uncertain, *White*, s.n. (RM).

MEXICO. **Tamaulipas:** Vicinity of San José, Mesa de Tierra, *Bartlett* 10405 (MICH).

Because *Rhus verrucosa* was described by Scheele, in order to typify the species a specimen was sought that he may have seen. McKelvey (1955) indicated that plants collected by Lindheimer in Texas in the middle decades of the eighteen hundreds were intended for Engelmann and Gray; any new species were to have been described by them. A number of specimens, however, went with Roemer to Germany and subsequently were described by Scheele in his series of articles under the title "Beitrage zur Flora von Texas." Unfortunately, no specimen representing *Rhus verrucosa* has been found at Heersum where Scheele was Pastor, nor at nearby Hildesheim, nor has any other specimen been found that could have been the one which Scheele examined.

Gray (1850) claimed that *Lindheimer* 346 (Fascicle iii) represented the species that Scheele (1848) had in mind when naming the plant. Scheele described the plant from New Braunfels whence Lindheimer made several collections, each distributed in several herbaria. It appears that all of the specimens in Table 4 represent Lindheimer's poison-ivy gatherings from New Braunfels.

If we can trust Lindheimer's numbering system, the 1847 and later collections must be excluded from considerations of a type, since, before the 1847 collections were made, Roemer took the specimens to Germany — specimens which Scheele described in 1848 (McKelvey, 1955). As Gray (1850) and Fernald (1941) decided, *Lindheimer* 346 probably represents the collection which Scheele had under consideration, but there are two collections so numbered. The collections given the same number in 1847 (added in longhand on a printed label which reads "fasc. iv. 1847") are probably intended to represent the same population, only a later collection, hence the same number. Since *Lindheimer* 401 of the regularly-numbered series is *Lagenaria vulgaris*, the handwritten labels numbered 401 for a poison-ivy no doubt

fall into the category which Blankinship (1907) indicated were specimens not collected in quantity, nor even in numbered exsiccatae, but are private Lindheimer numbers for the Engelmann Herbarium (now at MO). In Gray's listing, *Lindheimer* 245 of the regular series is *Sedum sparsiflorum* and 246 is miswritten as a typographical error: "346" (it appears in a consecutive list between 245 and 247 and hence must be intended to be 246); it is *Galium virgatum*. Hence, 245 and 246 are again examples of private numbers for the Engelmann Herbarium, not to be confused with the series of numbered exsiccatae.

The problem remains as to which specimen should be named lectotype. Lacking Scheele's specimen, a good candidate would be the one which was in Gray's possession at the time, inasmuch as Gray wrote that *Lindheimer* 346 was *Rhus verrucosa* of Scheele. At the Gray Herbarium, there is a pair of specimens which were obviously on the same sheet and separated only in relatively recent years. The sheet had two specimens and three labels on it originally. One specimen was probably part of the May 1845 gathering (according to one of the three labels), and the other a part of a September 1846 gathering. The printed label (associating the plants with Fasc. iii, *Lindheimer* 346) was superfluous originally since neither plant was part of the gathering which was distributed under the 346 number as we shall see. The specimen to which the printed label is affixed is now highly significant because it has been annotated "*Rhus verrucosa* Scheele" in Gray's handwriting. The specimen which has now been detached from Gray's annotation more nearly fits Scheele's description than the specimen which remains attached to it, however, and hence has been chosen lectotype (see Fig. 46.)

The excluded specimen mentioned above (No. 246) has been annotated *Rhus radicans* var. *rydbergii* by Fernald, but is more likely a sparsely pubescent *Toxicodendron radicans* subsp. *pubens*. Among other reasons for this choice is the fact that *T. rydbergii* does not occur in this part of Texas. It is indicated in Gray (1850) by a symbol used to designate specimens which were not distributed. A specimen

TABLE 4. LINDHEIMER COLLECTIONS FROM NEW BRAUNFELS, TEXAS

Collection Number	Stage	Date	Herbaria Where Found
245	sterile	August 1846	MO-1774755
246	fruiting	September 1846	GH, MO-1773729
Fascicle iii 346	fruiting	1846	GH, US-1814899, MO-1774754, MO-1774755
401	fruiting (few flowers)	May 1845	GH, MO-1774754
Fascicle iv 346	fruiting	1847	MIN-460085, MO-1773726
unnumbered	flowering	1850	KSC
unnumbered	fruiting	1851	MO-1774756

in the Engelmann Herbarium has the same printed label marked 346, but also has an attached label in Lindheimer's nearly illegible handwriting giving it collection number 401. The condition of the drupes on both of the 401 specimens suggests that they were not fresh at the time of collection, but had overwintered, thereby confirming their May date of gathering. The fruits of all other 346 specimens are fresher and were no doubt produced during the season of collection. At least one earlier worker at the Missouri Botanical Garden has noted on two specimens the idea that 346 = 401.

It is possible that all poison-ivy specimens that Lindheimer had on hand at the time of making his fascicle iii were included in the distribution under the number 346, whether they were collected in 1846 or before, especially if they were destined for Gray or Engelmann, his employers. Whether Scheele and Gray saw plants from the identical gathering can never be ascertained without an extant Scheele plant. What is assured, however, is that the May 1845 and the 346 gatherings have the insect chewings on the leaves which produced exudations of poison, now hardened into black specks. It was these which Gray maintained were the "verrucae magnae subrotundae atropurpureae lucidae" of Scheele's description, exudations which may have led Scheele to his choice of epithet "verrucosa." There is nothing else verrucose about any of the plants he could have had under consideration. Furthermore, the handwritten labels attached to the specimens which Gray examined declare them to be "small shrub on stony prairies" and "high, in thickets and climbing, N. Braunfels" in Engelmann's handwriting. These phrases agree with Scheele's "In Hecken auf felsen Boden auf Missionshugel bei Neubraunfels: Lindheimer."

I believe that the May 1845 collections (*Lindheimer* 401) distributed in part under exsiccatae number 346 with the date 1846 represent what Asa Gray had before him. The Engelmann Herbarium specimen under the same number is therefore an isolectotype. All other specimens distributed under the number 346 are considered to be topotypes

and therefore of interest, but not of nomenclatural significance.

Greene transferred *Rhus verrucosa* and *Rhus rhomboidea* to *Toxicodendron*. It is curious that he did not note the similarity of these two, both of which came from the same general region of Texas.

This subspecies is found on the Edward's Plateau of central Texas and the Arbuckle Mountains of Oklahoma, reaching its northern limit at Turner Falls, Murray County, Oklahoma. In northeastern and south central Texas, the subspecies is found off the Plateau, but more or less maintains its distinct glabrous and sharply lobed leaflets. There is little apparent intergrading with other taxa, although some is suspected.

Collections of subsp. *verrucosum* have occasionally been confused with subsp. *eximium*, probably because both taxa have lobed leaflets. The latter has pubescent fruits and leaves, whereas the former is glabrous. Furthermore, leaflets of subsp. *verrucosum* have acutely-angled lobes, whereas the lobes of leaflets of subsp. *eximium* are rounded.

This taxon grows in the variety of habitats like those of most of its related subspecies but it is most frequently found in limey soils: lithosols, talus, limestone gravels, limestone bluffs, etc. It is also a roadside weed, found on alluvial banks, forest borders, and even in oak-pine woods on fairly excessively drained acid soils. It has also been reported from thin soil over chalk in Dallas County, Texas. Its community relationships have not been extensively explored.

4i. **Toxicodendron radicans** subsp. **eximium** (Greene) Gillis, comb. nov. (Fig. 47.)

Toxicodendron eximium Greene, Leafl. Bot. Observ. Crit. 1: 123. 1905. *Rhus eximia* (Greene) Standley, Contr. U. S. Natl. Herb. 23: 668. 1923. *Rhus toxicodendron* var. *eximia* (Greene) McNair, Publ. Field Mus. Nat. Hist. 225 Vol. 4: 68. 1925. *Toxicodendron radicans* var. *eximium* (Greene) Barkley, Ann. Mo. Bot. Gard. 24: 435. 1937 (as *eximia*). Type: *Dr. Edward Palmer* 106, Mexico, State of Durango,

Fig. 47. *Toxicodendron radicans* ssp. *eximium.* Above: Large leaves from a shaded branch. Below: Smaller leaves from an unshaded branch of the same plant.

vicinity of the city of Durango. April-November, 1896. (US-305009, holotype; A, F, GH, MO-1774807, NY, isotypes).

Toxicodendron biternatum Greene, Leafl. Bot. Observ. Crit. 1: 124. 1905. Type: *V. Havard*, s.n., Eagle Nest on Rio Grande River (Presidio), Presidio County, Texas. 1881. (US-156164, holotype).

Vine or shrub with aerial roots; leaflets broadly ovate, deeply-cut, rounded, incised-dentate, sinuate-lobed, sometimes tending to be trilobate; scabrescent to velutinous above, velutinous to tomentose below, veins hirtellous. Terminal leaflet blade 1.1-13.0 cm long, 0.7-11.5 cm wide; petiole hispid, tomentose, or villous; terminal petiolule 0.1-4.5 cm long. Fruits 3-5 mm broad, glabrate, setose, or hispidulous, yellow-cream. Blade tip acute to acuminate, base cuneate.

Distribution: United States: southwestern Texas; Mexico: Coahuila, Durango, Tamaulipas. (Fig. 41.)

Representative specimens: UNITED STATES. **Texas.** BREWSTER CO.: Big Bend National Park, Chisos Mts., *Warnock* 1212 (ARIZ, GH, TEX); Willow Creek Canyon, *Sperry* 201 (US); *Palmer* 34076 (A, MO, NY); Goode Place, *Young*, s.n. (GH, TEX); Oak Canyon, *Cory* 7010, 18689 (GH); *Mueller* 8063 (F, TEX); Oak Canyon, base of Ward Mt., *Gillis* 5745 (MSC). MAVERICK CO.: Eagle Pass, *Havard*, s.n. (GH). PRESIDIO CO.: Camp Eagle Nest (Presidio), *Havard*, s.n. (US); Fresno Canyon, tributary of Mexican Canyon, *Hinckley* 3596 (SMU, U); Marfa, *Hinckley* 2646 (ARIZ, GH, NY); Shafter, Cibolo Canyon, *Hinckley* 2580 (A, ARIZ, NY, SRSC). VALVERDE CO.: Nueces River near Rio Grande, *Palmer* 33466 (A, MO, NY, US); High bridge of Pecos River, *Pilsbry*, s.n. (PH); Devils River, *Palmer* 13603 (A, MO, WIS); Devils River, *Traverse* 2146 (SMU).

MEXICO. **Coahuila:** Muzquiz, *Marsh* 1166 (GH); Sierra Hechiceros, *Stewart* 158 (GH). **Durango:** Near Durango (Nombre de Dios), *Palmer* 106 (A, GH, MO, NY, US). **Tamaulipas:** Victoria, *Palmer* 154 (US, A, GH, NY). El Rosario, vicinity of Marmolejo, *Bartlett* 10881 (MICH). **Nuevo León:** San Augustin, Monterrey, *Abbon* 246 (A, F, MO, US).

The type was collected a long distance from any other known stations for this subspecies. Greene (1905) indicates that it was collected at Nombre de Dios, 40 miles southeast of Durango. The type for *T. biternatum* was collected at Eagle Nest on the Rio Grande River. Barkley (1937) mapped this in Maverick County, Texas, but he

probably confused this locality with Eagle Pass. The actual locality was Camp Eagle Nest, where Havard was post surgeon from August 1880 until June 1881 (McVaugh, 1957). The camp has long since disappeared, but it occupied the present site of the city of Presidio in Presidio County. This flowering specimen must have been collected in the spring of 1881, although the type specimen indicates only "188 ."

This subspecies is one of the more unusual and rare forms of poison-ivy. It is found rarely along the Rio Grande River itself, but is more likely to be found in the washes and tributaries to that river. It apparently had not been collected between 1937 and 1964, at which time Dr. Barton Warnock helped me find a station that was known to him years earlier in Oak Canyon of the Chisos Mountains of Big Bend National Park. This plant is restricted to the canyon bottom where it is abundant, but no trace of it is found anywhere on the walls of the canyon, nor on the ridges above.

The subspecies is distinctive by its peculiarly lobed leaflets which often tend to be trilobate to the extent that they resemble the "club" on a deck of playing cards. The pubescence of the leaves and fruits suggests a relationship of *Toxicodendron toxicarium*, but the climbing habit and aerial roots require its placement in *T. radicans*. As is the case in other taxa, shade leaves are much smaller than sun leaves (sic), as shown in Fig. 47.

Superficially this taxon resembles *Toxicodendron radicans* subsp. *verrucosum* and has frequently been misidentified as such. Earlier maps of its distribution have been in error when they indicated its being found in central Texas, probably because of confusion with subsp. *verrucosum*, a more widely distributed taxon. (See discussion under *T. radicans* subsp. *verrucosum*.)

It is not easy to characterize the niche which is occupied by this plant for there have been few studies of its community associations. The only time that I have studied subsp. *eximium* in the field was in the one canyon bottom mentioned above. There it had the following assemblage of associates:

Fig. 48. *Toxicodendron rydbergii.* Holotype of *Toxicodendron fothergilloides* Lunnell, *Lunnell* 706.

Quercus gravesii, Garrya ovata, Juniperus flaccida, Rhus virens, Vitis arizonica, Arbutus texana, and *Ungnadia speciosa.* The soils in which it grew were shallow volcanic lithosols containing calcium concentrations of 1099 ppm.

5. **Toxicodendron rydbergii** (Small ex Rydberg) Greene. Fig. 48.

Rhus rydbergii Small ex Rydberg, Mem. New York Bot. Gard. 1: 268. 1900. *Toxicodendron rydbergii* (Small ex Rydberg) Greene, Leafl. Bot. Observ. Crit. 1: 117. 1905. *Rhus toxicodendron* var. *rydbergii* (Small ex Rydberg) Garrett, Spring Flora Wasatch Range, 3rd. ed., 68. 1917. *Rhus radicans* var. *rydbergii* (Small ex Rydberg) Rehder, J. Arnold Arbor. 20: 416. 1939. *Toxicodendron radicans* var. *rydbergii* (Small ex Rydberg) Erskine, Pl. Prince Edward Island, 190. 1961. Lectotype: *R. S. Williams* 291, Montana, Cascade Co., Great Falls, 1885 (NY). Lectoparatype: *F. W. Anderson,* s.n., northern Montana, Helena, Lewis and Clark Co. (NY).

Rhus toxicodendron var. *vulgare* Michx., Fl. Bor. Am., 183. 1803. *Rhus toxicodendron vulgaris* a. *radicans* Engler in DC., Monogr. Phaner. 4: 394. 1883. *Rhus radicans* var. *vulgaris* Roemer et Schultes, Sys. Veg. Vol. 6. 1820, non *Toxicodendron vulgare* Miller, Gard. Dict., Art. *Toxicodendron,* No. 1. 1768. Type: "Hortus parisiensis," lectotype (P).

Toxicodendron macrocarpum Greene, Leafl. Bot. Observ. Crit. 1: 117. 1905. Type: *C. H. Thompson* 102, Kansas, Hamilton Co., 11 July 1893 (US-265734, holotype).

Toxicodendron longipes Greene, Leafl. Bot. Observ. Crit. 1: 118. 1905. Type: *Lester F. Ward* 212, Canyon south of Glenwood, Sevier Co., Utah, altitude 6300 feet, 12 June 1875 (US-153641, holotype).

Toxicodendron hesperium Greene, Leafl. Bot. Observ. Crit. 1: 118. 1905. Type: *Kirk Whited* 241, Washington, Chelan Co., Wenatchee, 6 August 1893 (1896?) (US-268197, holotype).

Toxicodendron pumilum Greene, Leafl. Bot. Observ. Crit. 1: 124. 1905, non *T. pumilum* Kuntze, Rev. Gen. Pl. pt. 1,

154. 1891. Type: *D. T. MacDougal* 28, Arizona, Coconino Co., vicinity of Flagstaff, altitude 7000 feet, 28 June 1898 (US-334125, holotype; F-69784, GH, NDA, NY, RM-31903, isotypes).

Toxicodendron punctatum Greene, Leafl. Bot. Observ. Crit. 1: 125. 1905. Type: *O. B. Metcalfe* 1088, New Mexico, Sierra Co., Black Range, near Kingston, 9 July 1904 (US-498281, holotype; F-187484, GH, MIN-294394, MO-1773740, NY, US-890258, isotypes).

Toxicodendron desertorum Lunell, Amer. Midl. Naturalist 2: 185. 1912. Type: *J. Lunell,* s.n., North Dakota, McHenry Co., gravelly soil sand hills, 13 July 1899 (MIN-245797, holotype).

Toxicodendron fothergilloides Lunell, Amer. Midl. Naturalist 2: 186. 1912. Type: *J. Lunell* 706, Ramsay Co., North Dakota, thickets at Devil's Lake, 29 June 1902 (MIN-245796, holotype).

Sub-shrub often less than 1 meter high to shrub up to 3 meters. Stem simple or sparsely upright-branched, arising from much branched subterranean stolons; aerial roots absent, plant never climbing. Leaves approximate near summit of stem, often appearing falsely verticillate. Terminal leaflet blade broadly ovate, rhomboid or suborbicular and usually acuminate, 3.0-15.0 cm long, 2.0-11.0 cm wide; petiole glabrous (-glabrate), 1.5-25.0 cm long; terminal petiolule 0.6-5.5 cm long. Leaflet margins dentate or undulate, subtruncate or rounded at the base, glabrous above, often with a line of minute, curly hairs along the midrib, glabrous or appressed strigose below; autumn coloration generally yellow to orange, less often bronze or red. Flowers in small clusters. Fruit globose, cream to yellow, (3-) 4-7 mm broad, glabrous, smooth.

Distribution: Canada: southern provinces north to 52° N. Lat. United States: central Washington, Oregon, Utah south to northeastern Arizona and western Texas, east to central Kansas, Nebraska, Iowa, southern Wisconsin, northern Michigan, New York, New England; few mountain tops,

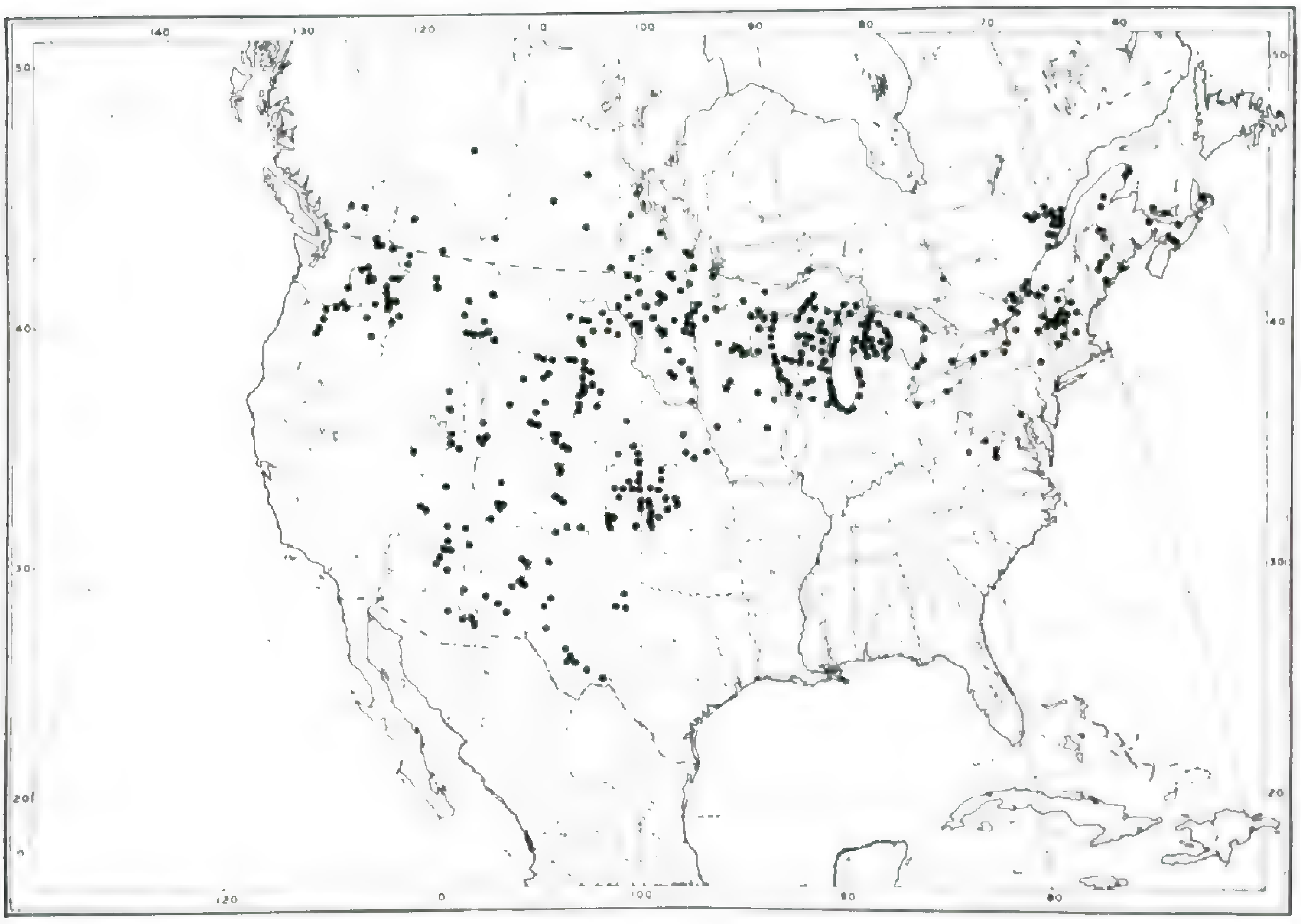


Fig. 49. Distribution of *Toxicodendron rydbergii.*

Appalachian Mountains. Common name: Rydberg's poison-ivy, poison-oak (erroneously). (Fig. 49.)

Representative specimens: UNITED STATES. **Arizona.** APACHE CO.: Bog Creek, 8 miles east of McNary, *Deaver* 6391 (ARIZ). COCHISE CO.: Big Emigrant Canyon, *Blumer*, s.n. (ND-G, NY); Chaperon Canyon, *Blumer* 1325 (ARIZ, E, F, GH, KSC, MIN, MO, ND-G, NY, RM, US); Cabeyas Mts., *Simmon* 160 (GH); Fort Huachuca, *Wilcox* 215 (US); Chiricahua National Forest, *Burrall* 2029 (US). COCONINO CO.: bottom, West Fork Canyon, Oak Creek Canyon, near Sedonia, *Demaree* 41258 (ARIZ); Bright Angel Canyon, *Nelson* 125 (US). GILA CO.: Parker Creek Branch Station, *Little* 4007 (ND). NAVAJO CO.: Betatakin ruins, *Howell* 24569 (ARIZ); Fort Apache, *Mayerhoff* 47 (F). PIMA CO.: Coronado National Forest, *Clark* 4852 (SMU). SANTA CRUZ CO.: Santa Rita Forest Reserve, *Griffiths* 4222 (US). YAVAPAI CO.: Montezuma Well near Camp Verde, *Gillis* 6602 (MSC, US). **Colorado.** BOULDER CO.: Gregory Canyon near Boulder, *Robbins* 1607 (RM). DENVER CO.: Denver, *Smith*, s.n. (KSC). EL PASO CO.: Pikes Peak, *Ball*, s.n. (US); Williams Canyon, *Harper & Harper*, s.n. (A). LARIMER CO.: Canyon of the Thompson near Forks, *Osterhout* 3631 (RM). LAS ANIMAS CO.: Region of the Mesa de Maya, Troy, *Rogers* 6025 (TEX, US). MESA CO.: Grand Junction, *Eastwood* 7217 (A). SAN MIQUEL CO.: Norwood Hill, *Walker* 498 (GH, MIN, NY, RM, US). MONTEZUMA CO.:

Navajo Canyon, Mesa Verde, *Cary* 181 (US). WELD CO.: Windsor near river, *Osterhout* 1725 (ND-G, RM). **Idaho.** BONNER CO.: Big Potlatch River, *Christ* 4275 (NY). VANNOCK CO.: Inkom, *Jack* 1142 (A). BONNER CO.: Lake Pen D'Oreille, *Christ* 11181 (NY). BOUNDARY CO.: Bonner's Ferry, *Epling* 10465 (MO). IDAHO CO.: Cottonwood, *Christ* 10062 (NY). KOOTENAI CO.: Coeur d'Alene, *Christ* 19126 (NY). LATAH CO.: Julietta, *Christ* 10157 (NY). LEMHI CO.: Indianola Ranger Station, *Hitchcock & Muhlick* 14324 (NY). **Illinois.** COOK CO.: Glencoe, shore of Lake Michigan, *Churchill*, s.n. (MIN). DU PAGE CO.: Wheaton, *Moffatt* 594 (WIS). LAKE CO.: Waukegan, *Steyermark & Standley* 28186 (F). **Indiana.** BENTON CO.: Pine, *Merner* 14907 (WIS). LAKE CO.: Gary, *Thieret* 1505 (F). LAPORTE CO.: wooded dunes 2 miles west of Michigan City, *Deam* 8854 (IND). MARSHALL CO., Lake Maxinkuckee, *Evermann* 833 (US). PORTER CO.: Dunes State Park, *Tryon* 1071 (F). **Iowa.** CERRO GORDO CO.: Mason City, *Shimek*, s.n. (NY). CLAYTON CO.: Giard, Grether 8136 (WIS). DICKINSON CO.: Spirit Lake, *Evermann*, s.n. (F). JOHNSON CO.: Lake Macbride State Park, *B.C.G.* 64763 (FSU). **Kansas.** (All Hitchcock collections are without definite locality.) COMMANCHE CO.: *Hitchcock*, s.n. (KSC). COWLEY CO.: locality unknown, *Clothier & Whitford*, s.n. (KSC). DECATUR CO.: *Hitchcock*, s.n. (KSC). DICKINSON CO.: *Westgate*, s.n. (KSC). DOUGLASS CO.: *Hitchcock*, s.n. (KSC). ELLSWORTH CO.: Ellsworth, *Palmer* 21289 (US). HAMILTON CO.: Syracuse, *Thompson* 102 (GH, KSC, MO, US). KEARNEY CO.: *Hitchcock*, s.n. (KSC). KIOWA CO.: *Hitchcock*, s.n. (KSC). LEAVENWORTH CO.: *Hitchcock*, s.n. (KSC). LOGAN CO.: *Hitchcock*, s.n. (KSC). MARSHALL CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). MCPHERSON CO.: Lindsberg, Bodin, s.n. (MIN). MEADE CO.: *Hitchcock*, s.n. (KSC). MORTON CO.: *Hitchcock*, s.n. (KSC). NESS CO.: *Hitchcock*, s.n. (KSC). OSBORNE CO.: Osborne City, *Shear* 226 (RM, US). PAWNEE CO.: *Hitchcock*, s.n. (KSC). POTTAWATOMIE CO.: St. George, *Kellerman*, s.n. (MO). PRATT CO.: without definite locality, *Van Vranken* 183 (KSC). RENO CO.: *Hitchcock*, s.n. (KSC). REPUBLIC CO.: without definite locality, *Smith*, s.n. (KSC). RUSH CO.: *Hitchcock*, s.n. (KSC). RUSSELL CO.: without definite locality, *Hutchinson* 278 (KSC). SALINE CO.: Salina, *Hancin* 2426 (KSC). SHERIDAN CO.: *Hitchcock*, s.n. (KSC). STANTON CO.: *Hitchcock*, s.n. (KSC). SUMNER CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). THOMAS CO.: *Hitchcock*, s.n. (KSC). TREGO CO.: *Hitchcock*, s.n. (KSC). WALLACE CO.: *Hitchcock*, s.n. (KSC). WEBSTER ROCK CO.: without definite locality, *Griebel*, s.n. (KSC). WICHITA CO.: *Hitchcock*, s.n. (KSC). **Maine.** AROOSTOOK CO.: Fort Fairfield, *Fernald* 1995 (GH). KENNEBEC CO.: Winthrop, *Sturtevant*, s.n. (MO). LINCOLN CO.: Boothbay, *Fassett* 28979 (SMU). SOMERSET CO.: Fairfield, *Fernald & Long* 14017 (GH). WASHINGTON CO.: Ox Cove, *Fernald* 1993 (GH). **Massachusetts.** BERKSHIRE CO.: Berkshire, *Churchill*, s.n. (MO). **Michigan.** ALCONA CO.: Crooked Lake, *Gillis* 4136 (MSC). ALGER CO.: Au Train Lake, *Gillis* 3643 (MSC); Devil's Slide, *Gillis* 5549

(MSC). ALLEGAN CO.: Old Baldy Dune near Saugatuck, *Gillis* 3523 (MSC). ALPENA CO.: Long Rapids Twp., *Gillis* 4123 (MSC). ANTRIM CO.: Eastport, *Gillis* 3629 (MSC). BARAGA CO.: Sturgeon River, *Gillis* 3114 (MSC). BENZIE CO.: Point Betsie, *Gillis* 6511 (MSC). CHARLEVOIX CO.: Charlevoix on dunes, *Gillis* 2940 (MSC); Beaver Island, *Ries*, s.n. (BLH). CHEBOYGAN CO.: University of Michigan Biological Station, *Gillis* 2943 (MSC). CHIPPEWA CO.: De Tour, *Gillis* 4117 (MSC); Drummond Island, *Hiltunen* 1809 (MSC, WUD); Sugar Island, *Hiltunen* 261 (WUD). CRAWFORD CO.: Lake Margrethe, *Gillis* 3074 (MSC); Wakeley Bridge, *Gillis* 5513 (MSC). DELTA CO.: base of Burnt Bluff, *Gillis* 3645 (MSC). DICKINSON CO.: Quinnesec, *Gillis* 3069 (MSC); EMMET CO.: Mackinac City, *Gillis* 3073 (MSC). GOGEBIC CO.: Gogebic Lake, *Darlington*, s.n. (MSC). GRAND TRAVERSE CO.: East Bay near Acme, *Gillis* 2802 (MSC); mixed woods below Brown Bridge Dam on bank of Boardman River, *Dieterle* 1722 (MICH). HOUGHTON CO.: Bear Lake, *Richards* 3996 (MICH, MIN, NY). IOSCO CO.: Nissikone Camp for Boys, *Gillis* 3532 (MSC). IRON CO.: Horserace Rapids, *Gillis* 3041 (MSC). KENT CO.: Ross, *Jones*, s.n. (MO). KEEWENAW CO.: Anich, *Farwell*, s.n. (MSC). LAKE CO.: Pine River, Dover Twp., *Gillis* 3620 (MSC). LEELANAU CO.: Seeping Bear Dune, base of pinnacle, *Gillis* 3489 (MSC); South Manitou Island, morainic bluff, *Voss* 9878 (MICH). LUCE CO.: Manistique Lake shore, *Gillis* 3639 (MSC). MACKINAC CO.: St. Ignace, *Gillis* 3638 (MSC); Thuja forest, Mackinac Island, *Potzger*, 7308 (ND). MANISTEE CO.: Portage Park dunes, *Umbach* 8401 (MICH). MARQUETTE CO.: Tankowa Lake, *Gillis* 5473 (MSC). MASON CO.: Ludington, dunes, *Chase* 12553 (ILL, NY). MENOMINEE CO.: shore of Lake Michigan along highway, *Waterman* 372 (MSC). MISSAUKEE CO.: Hopkins Creek, *Gillis* 3538 (MSC); Goose Lake, *Gillis* 3537 (MSC). MONTMORENCY CO.: West Twin Lake, *Gillis* 5517 (MSC). MUSKEGON CO.: near Coast Guard Station near North Muskegon, *Gillis* 5398 (MSC). OCEANA CO.: Pentwater dunes, *Chase* 12713 (ILL). OGEMAW CO.: Piper Lake, *Gillis* 3534 (MSC). ONTONAGON CO.: Escarpment overlooking Lake-of-the-Clouds, *Gillis* 3152 (MSC). OSCODA CO.: Mio, *Gillis* 4140 (MSC). OTSEGO CO.: Otsego Lake, *Gillis* 3631 (MSC). OTTAWA CO.: Ferrysburg dunes, *Gillis* 3528 (MSC). PRESQUE ISLE CO.: Rogers City, *McVaugh* 9228 (BLH, MO, MICH). ROSCOMMON CO.: Roscommon, *Gillis* 3536 (MSC). SCHOOLCRAFT CO.: Hiawatha National Forest, shore of Clear Lake, *Waterman* 361 (MSC). WEXFORD CO.: Greenwood Twp., above Manistee River on High Roll Way, *Gillis* 3626 (MSC). **Minnesota.** BECKER CO.: Detroit, *Woladron*, s.n. (NDA). CARLTON CO.: Thompson, *Sandberg* 541, (KSC, MISC). CARVER CO.: without definite locality, *Anthony & Waconia*, s.n. (WIS). CLAY CO.: Buffalo State Park, *Schuette* s.n. (GH). DAKOTA CO.: without definite locality, *Moore & Moore* 16214 (BRY). ITASCA CO.: Bena *Gillis* 3176 (MSC); Sand Lake, *Johnson* 2122 (MO). JACKSON CO.: Kilen Woods State Park, *Moore & Huff* 19341 (SMU). LAKE OF THE WOODS CO.: without definite

locality, *Moore & Moore* 12166 (NDA). MARSHALL CO.: Warren, *Gillis* 3177 (MSC). NORMAN CO.: Frenchman's Bluff, *Stevens*, s.n. (NDA). RAMSEY CO.: St. Paul, St. Anthony Park, *Lugger*, s.n. (NDA). ST. LOUIS CO.: Duluth, *Lakela*, s.n. (F, NY, US); STEARNS CO.: Paynesville Twp., *Moore & Phinney* 12639 (A). WINONA CO.: Winona, *Holzinger*, s.n. (GH). **Montana.** CASCADE CO.: Great Falls, *Williams* 291 (NY, US). DAWSON CO.: Glendive, *Ward*, s.n. (US). FLATHEAD CO.: Flathead Lake, *Clemens*, s.n. (F). GALLATIN CO.: Bozeman, *Blankinship* 106 (F, MO, US). LAKE CO.: Swan Lake, *Jack* 2377 (A). LEWIS AND CLARK CO.: Helena, *Anderson*, s.n. (NY). MADISON CO.: Upper Madison River, *Lenz*, s.n. (MO, ND). PARK CO.: Livingston, *Booth* 3802 (NDA). STILLWATER CO.: Absarokee, *Hawkins*, s.n. (WIS). **Nebraska.** BROWN CO.: Columbus, *Palmer* 36060 (MO, NY). DIXON CO.: Newcastle, *Clements* 2606 (NY, US). FRANKLIN CO.: Franklin, *Laybourn* 47 (M). GAGE CO.: without definite locality, *Knight*, s.n. (RM). KEARNEY CO.: Minden, *Hapeman*, s.n. (ARIZ, FLAS, MIN, MO, RM, SMU). OTOE CO.: Syracuse, *Osborn* 762R (MO). SALINE CO.: Crete, *Diehl*, s.n. (BRY). SHERIDAN CO.: Metcalf Public Hunting Grounds, 13 miles north of Hay Springs, pine forest, *Nixon* 53 (RM). SIOUX CO.: Monroe Canyon, *Baker*, s.n. (MO). STANTON CO.: Stanton, *Lindbo*, s.n. (US). THOMAS CO.: Helsey sand hills, *Breneckle*, s.n. (NDA). **New Hampshire.** CARROLL CO.: Intervale, between Conway and Bartlett, *Rehder* 997 (A, US). COOS CO.: Shelburne, *Moore* 4171 (GH). GRAFTON CO.: Thornton along railroad, *Gillis* 4098 (MSC); Warren, *Williams*, s.n. (GH). HILLSBORO CO.: Fox State Forest, *Baldwin*, s.n. (MSC); **New Mexico.** BERNALILLO CO.: Capelin Canyon, Sandia Mts., *Ellis* 245 (MO, NY, US). CATRON CO.: Gila River west fork, *Metcalfe* 339 (GH). COLFAX CO.: Ute Park, *Standley* 14036 (US). LINCOLN CO.: Gray, *Earle & Earle* 485 (NY); Ruidosa Creek on Mescalero Reservation, 7 miles west of Ruidosa, *Hinckley* 780 (ARIZ, F, GH, NY, SRSC, TEX). SANDOVAL CO.: Tijeras Canyon, Sandia Mt. north end, *Stoutamire* 3979 (MSC). SAN MIQUEL CO.: Pecos River Division, Santa Fe National Forest, *Standley* 4011 (GH, NY, RM, US). SIERRA CO.: Kingston, *Metcalfe* 1088 (F, GH, MIN, MO, NY, US). SOCORRO CO.: Gila River, Mogollon Mts., *Metcalfe* 339 (ARIZ, E, MIN, MO, ND-G, NY, RM, US); **New York.** ESSEX CO.: Port Henry, *Britton*, s.n. (NY). MONROE CO.: Inspiration Pt., *Matthews* 2131 (WIS). NIAGARA CO.: Niagara Falls at base of Bridal Veil Falls, *Gillis* 6316 (MSC). ONONDAGA CO.: near Syracuse, *Underwood*, s.n. (E). OSWEGO CO.: Selkirk, *Fernland, Eames, & Wiegand* 14374 (GH). ST. LAWRENCE CO.: Lisbon, *Phelps* 642 (GH, NY). ULSTER CO.: Lake Mohonk, *Gillis* 4061 (MSC). WARREN CO.: The Glen Pack Forest, *Gillis* 5378 (MSC). WASHINGTON CO.: Pilot Knob Lake George, *House* 28972 (TEX). **North Carolina.** CUMBERLAND CO.: Fayetteville, *Miles*, s.n. (US). **North Dakota.** BARNES CO.: Valley City, *Bergman* 393 (NDA). BENSON CO.: Butte, *Lunell*, s.n. (NY); Pleasant Lake, *Lunell*, s.n. (MIN). BILLINGS CO.: Medora in ravine,

Bergman, s.n. (NDA). BOTTINEAU CO.: Lake Metigoshe, *Stevens*, s.n. (NDA). BURLEIGH CO.: Bismarck, Apple Creek, *Stevens*, s.n. (NDA). CASS CO.: Fargo along Red River, *Bergman*, s.n. (NDA). CAVALIER CO.: Tongue River, *Stevens*, s.n. (NDA). DUNN CO.: Killdeer Mts., *Stevens & Moir*, s.n. (NDA). EDDY CO.: Hamar, *Stevens*, s.n. (NDA). EMMONS CO.: Linton, *Stevens*, s.n. (NDA). GOLDEN VALLEY CO.: Sentinel Butte, *Bergman*, s.n. (NDA). GRAND FORKS CO.: Turtle River State Park, *Stevens*, s.n. (NDA). GRANT CO.: Wade, *Bell*, s.n. (NDA). KIDDER CO.: Dawson State Game Refuge sand flat, *Stevens*, s.n. (NDA). LOGAN CO.: Napoleon, *Stevens*, s.n. (NDA). LAMOURE CO.: Kulm, *Brenckler*, s.n. (NDA). MCHENRY CO.: Sand Hills, *Lunell*, s.n. (MIN). MCLEAR CO.: T. 48, R. 91 woods, *Heidenreich*, s.n. (NDA). MORTON CO., Mandan, *Bergman*, s.n. (NDA). OLIVER CO.: Fort Clark, *Hayden*, s.n. (MO). PEMBINA CO.: Walhalla stream bank, *Bergman* 1965 (NDA, OSC). PIERCE CO.: Lake Girard, lower edge of prairie coulee, *Stevens*, s.n. (NDA). RAMSAY CO.: Devil's Lake, *Lunell* 706 (MIN, RM, WIS). RANSOM CO.: McLeod, *Stevens*, s.n. (NDA). RICHLAND CO.: Hankinson, lake shore, *Bergman* 804 (NDA); Kindred, sandy prairie, *Stevens* 2465 (NDA). ROLETTE CO.: Duneith, *Stevens*, s.n. (NDA). SARGENT CO.: Milnor, *Stevens*, s.n. (NDA). SHOPE CO.: Black Butte in coulee, *Stevens & Moir*, s.n. (NDA). STARK CO.: Hebron, side of butte, *Stevens & Moir*, s.n. (NDA). WARD CO.: Minot, *Lakela* 389 (MIN). WELLS CO.: NE slope of Coteau, *Stevens*, s.n. (NDA). WILLIAMS CO.: Williston, *Bell* 191 (NDA). **Ohio.** ASHTABULA CO.: Geneva-on-the-Lake, *Rood* 2484- (MIN). **Oklahoma.** BEAVER CO.: Knowles, *Stevens* 516 (MO). **Oregon.** BAKER CO.: Wallowa National Forest, *Peterson* 236 (OSC). BONNER CO.: Kootenay, *Lyall*, s.n. (GH). DESCHUTES CO.: Redmond, *Whited* 122 (ND). GRANT CO.: Canyon City, *Peck* 10174 (NY). JEFFERSON CO.: west of Culver on bank of Crooked River, *Gillis* 5215 (MSC); Warm Springs, *Gillis* 4218 (MSC). SHERMAN CO.: Rufus, *Gillis* 4227 (MSC). UMATILLO CO.: Pendleton, *Henderson* 29 (GH). WALLOWA CO.: Snake River Canyon, Eureka Creek, *collector unknown*, (WTU); College Creek Ranger Station, *Ingram* 2940 (ND). WASCO CO.: Maupin, *Gillis* 4217 (MSC). **Pennsylvania.** LANCASTER CO.: Lancaster, *Ely*, s.n. (MIN). **South Dakota.** BROOKINGS CO.: Brookings, *Moore* 59 (MIN). CLAY CO.: floodplain of Brule Creek, 12 miles east of Vermilion, *Over* 7020 (SDU). CUSTER CO.: Hermosa, *Rydberg* 594 (NY, US); Jewel Cave National Monument, *Stoutamire* 4004 (MSC). DAVISON CO.: Mitchell, *Small*, s.n. (F). FALL RIVER CO.: Edgemont, *Visher* 2569 (F, RM, SDU); Hot Springs, *Thatcher* 129 (MIN). HANSON CO.: Alexandria, *Weber*, s.n. (FLAS). HARDING CO.: Cave Hills, *Moore* 1823 (MIN). KINGSBURY CO.: Spirit Lake, *Thornber*, s.n. (ARIZ). LAWRENCE CO.: Deadwood, *Carr* 83 (F, MIN, MO, NY, SDU, US, WIS). MEADE CO.: Ft. Meade, *Forwood* 60 (US); Piedmont, *Pratt* 6116 (F, MIN, RM, WIS). MINNEHAHA CO.: Sand Hills, *Duncan*, s.n. (MIN). PENNINGTON CO.: Rockerville, *White*, s.n. (MO); Dark Canyon, 7

miles west of Rapid City, *McIntosh* 676 (SDU). SHANNON CO.: White River Valley, *Visher* 2184 (NY). SPINK CO.: Mellette, *Brenckle* 41-28 (FLAS, MO, NY). STANLEY CO.: Cedar Pass, *Over* 6081 (SDU). **Texas.** ARMSTRONG CO.: Gamble's Ranch, *Palmer* 13928 (GH, MO). BREWSTER CO.: Alpine, *Warnock* 8409 (SMU); Pine Peak, Davis Mts., *Hinckley* 1107 (ARIZ, F). BRISCOE CO.: Lubeck, *Demaree* 7629 (MO). CULBERSON CO.: McKittrick Canyon, *Hinckley* 4484 (SRSC). FLOYD CO.: between Floydada and Emma, *Coville* 1879 (US). JEFF DAVIS CO.: 10 miles SE of Fort Davis, *Cory* 53563 (SMU, US); Elbow Canyon near Pine Peak, *Hinckley* 1107 (ARIZ, GH, NY, TEX). **Utah.** CACHE CO.: Logan, *Cotten*, s.n. (MIN). DAGGETT CO.: Grouse Creek Canyon, *Graham* 8115 (GH, MO). DAVIS CO.: Farmington, *Clemens*, s.n. (A, GH). JUAB CO.: without definite locality, *Maguire & Holmgren*, s.n. (GH, NY). SALT LAKE CO.: City Creek Canyon, Salt Lake City, *Palmer* 38032 (M). SEVIER CO.: Glenwood, *Ward* 212 (US). SUMMIT CO.: Wahsatch, *Watson* 218 (US). UINTAH CO.: Ashley Creek near mouth of Dry Fork, *Graham* 6766 (MO); Split Mt. Gorge, Dinosaur National Monument, *Welsh* 367 (BRY). WASHINGTON CO.: Springdale, *Jones* 5249 (MIN, MSC, MO, US); Zion National Park, springline on Cathedral Mt., *Gillis* 6632 (MSC, US). **Vermont** ADDISON CO.: Leicester, *Dutton*, s.n. (FLAS); CALDEONIA CO.: Barnet, *Blanchard*, s.n. (MIN, MO, US). CHITTENDEN CO.: Charlotte, *Hosford*, s.n. (F). LAMOILLE CO.: Cambridge Junction, *Donahue* 272 (MSC). ORANGE CO.: Bradford, *Gillis* 4092 (MSC). ORLEANS CO.: Willoughby Lake, *Churchill*, s.n. (GH, MIN, MO). RUTLAND CO.: Proctor, *Banker* 247 (NY). WINDHAM CO.: Westminster, *Gillis* 4081 (MSC). **Virginia.** GREENE CO.: summit of Rocky Mount near Skyline Drive, *Ewan* 17205 (TEX). PAGE CO.: Luray, *Steele & Steele* 151 (E, GH, MIN, MO, NY, US). **Washington.** CHELAN CO.: Chelan, *Muenscher & Muenscher* 11224 (A); Wenatchee, *Whited* 241 (US). GRANT CO.: Dry Falls, Coulee City, *Thompson* 9115 (GH, MO, ND, NY); Grand Coulee, Soap Lake, *Eyerdam* 625 (A, F, MO). KLICKITAT CO.: near John Day Dam on bluffs overlooking Columbia River, *Gillis* 5245 (MSC). OKANOGAN CO.: Epsom Lake, Kruger Mt. Oroville, *St. John, Courtney, & Parker* 5478 (WTU). SPOKANE CO.: Hangman Creek, *Suksdorf* 264 (GH); STEVENS CO.: Northport, on Columbia River, *Rogers* 640 (MO, NY, SMU). WALLA WALLA CO.: Waitsburg, *Horner* 129 (GH, US). WHITMAN CO.: Revere, *Eastwood* 13271 (A); Wawawai, *Elmer* 778 (A, ILL, MIN, MO, US, NY); YAKIMA CO.: N. Yakima, *Mosier*, s.n. (US). **West Virginia.** MINERAL CO.: Allegheny Front Mt., *Gillis* 5717 (MSC). UPSHUR CO.: Buckhannon, *Pollock*, s.n. (MO). **Wisconsin.** BARRON CO.: Poskin Lake, *Cheney*, s.n. (WIS); BAYFIELD CO.: Tomahawk Lake, *Fassett* 9814 (WIS); Port Wing, *Cheney* 7168 (WIS); BROWN CO.: Green Bay, Brannery Hill Creek, *Khuschke*, s.n. (MIN). BUFFALO CO.: near Fountain City, *Smith* 7147 (MIL, WIS). BURNETT CO.: Viola Lake, *Fassett* 9891 (WIS). CLARK CO.: Neillsville, *Goessl* 1493 (MIL). COLUMBIA CO.: near Prairie du Sac Bridge, *Smith* 8043

(A, MIL, WIS); DANE CO.: Beeche's Woods between Sauk City and Mazomanie, *Fassett* 21549 (MIN, WIS). DOOR CO.: Washington Island, *Fuller* 1429 (MIL); Sturgeon Bay, *Goessl* 3717 (MIL). DOUGLAS CO.: upper St. Clair Lake, *Museum Expedition*, s.n. (MIL). DUNN CO.: Menomonie, *Goessl* 9226 (MIL). EAU CLAIRE CO.: Eau Claire, *Goessl* 1715 (MIL); FLORENCE CO.: bank of Menominee River near Menominee, Michigan, *Gillis* 3061 (MSC); Fond du Lac, Moon Lake, *Smith & Fuller* 1810 (MIL). GRANT CO.: Bascobel, *Sylvester*, s.n. (MIL). IOWA CO.: Arena, *Bullamore*, s.n. (WIS); JACKSON CO.: Black River Falls, *Smith* 6894 (MIL, WIS). LACROSSE CO.: Mormon Coulee, *Harmon* 531 (WIS); LAFAYETTE CO.: near Belmont, *Smith* 7761 (A, MIL, WIS). LANGLADE CO.: Hollister, *Seymour* 10776 (WIS); LINCOLN CO.: Pine River Twp., *Seymour* 14055 (WIS); MARATHON CO.: Wassau, *Goessl* 2848 (MIL). MARINETTE CO.: east of Amberg, *Martz* 226 (WIS). MILWAUKEE CO.: Wauwatosa, *Finger*, s.n. (MIL). OCONTO CO.: Pensaukee, *Goessl* 4017 (MIL). ONEIDA CO.: Rainbow Rapids, *Cheney* 1351 (MIL, WIS). OZAUKEE CO.: Saukville Twp., *Kruschke* K-60-40 (MIL). PIERCE CO.: Prescott, *Museum Expedition*, s.n. (MIL). PRICE CO.: Fifield, *Graenicher*, s.n. (MIL). RACINE CO.: Horlicksville, *Wadmond* 466 (MIN); RICHLAND CO.: Richland, *Fassett* 22498 (GH, MO, WIS). SAUK CO.: Ableman, *Palmer* 27657 (A, MO); SHAWANO CO.: Shawano, *Goessl* 4760 (MIL). SHEBOYGAN CO.: Sheboygan, *Goessl*, s.n. (WIS); VERNON CO.: Genoa, *Museum Expedition*, s.n. (MIL); WASHBURN CO.: Minong, near Bass Lake, *Fassett* 8528 (A, GH, WIS, US). WAUSHARA CO.: Plainfield, *Fassett* 21637 (MO, WIS). WOOD CO.: Remington, *Fassett, Catenhusen, Grange, & Oehmeke* 20321 (WIS). **Wyoming.** ALBANY CO.: Pole Creek Canyon, *Nelson* 154 (GH, MIN, ND-G). CARBON CO.: Freezecut Hills, *Nelson* 4857 (MO, NY, RM); Seminoe Dam, N. Platte River, *Porter & Porter* 8525 (RM). CROOK CO.: Hulett, *Ownbey* 556 (RM). FREMONT CO.: 10 miles west of Lander, middle fork of Popo Agrie Creek, *Porter* 5569 (RM). HOT SPRINGS CO.: Wind River Canyon, south of Thermopolis, *Jones* 23840 (MSC). LARAMIE CO.: Pole Creek near Table Mt., *Nelson* 154 (RM). NATRONA CO.: Casper Mt., Garden Creek Falls, *Joswik* 301 (RM). PLATTE CO.: 15 miles west of Wheatland, Palmer Canyon, *Porter* 4415 (RM, SMU, TEX). SHERIDAN CO.: Big Horn, *Tweedy* 2289 (NY); Sheridan, *Rollins* 558 (GH, MO, NY). UINTA CO.: *Evanston, Pannel & Blackwood* 3630 (MO). WASHAKIE CO.: north end of Tensleep Canyon, Big Horn Range, *Porter & Porter* 8247 (RM).

CANADA. **Alberta.** Fort Saskatchewan, *Turner*, s.n. (ALTA). Medicine Hat, *Dore*, 11956 (MSC). **British Columbia.** International boundary between Kettle and Columbia Rivers, *Macoun* 63750 (ND-G), Spence's Bridge, *Macoun*, s.n. (NY). Fort Vancouver, *Hooker*, s.n. (K). **Manitoba.** Grand Rapids, *Scoggan* 4751 (MIN). Arveme, *Criddle*, s.n. (A). Vorette, Chainaie, St. Boniface, *Boivin* 6434 (MSC). Winnepegosis, *collector unknown* (WIN). Big Grass Marsh, south-

ern Lake Winnipeg, *collector unknown* (WIN). **New Brunswick.** CARLETON CO.: Woodstock, *Dore & Gorham* 45894 (US). VICTORIA CO.: Aroostook River, *Williams*, s.n. (GH). WESTMORELAND CO.: Cap Brulé, *Knowlton*, s.n. (GH). **Nova Scotia.** HALIFAX CO.: Shubenacadie Grand Lake, *Fernald & Bissell* 21787 (GH). HANTS CO.: Five Mile River, *Pease & Long* 21789 (GH). LUNENBURG CO.: Bridgewater, *Fernald & Long* 24093 (A, GH). PICTOU CO.: Ferrona Junction, *Robinson* 522 (NY). VICTORIA CO.: Port Bevis, *Fernald & Long* 21792 (GH). **Ontario.** ALGOMA CO.: Batchawana Falls, *Taylor et al.* 914 (GH). BRUCE CO.: Sydney Bay, *DeJong* 1355 (MSC); Stokes Bay, *Krotkov* 9193 (MO, NY). CARLETON CO.: Ottawa, *Marshall*, s.n. (MSC). FRONTENAC CO.: Westbrook, *Gillis* 5373 (MSC). Lambton, Pinery Provincial Park near Grand Bend, *Gillis* 5389 (MSC). LENOX CO.: Newburgh, *Baker*, s.n. (F). MANITOULIN CO.: Manitoulin Island, *Grassl* 5745 (NY). RENFREW CO.: Cobden, *Gillis* 3442 (MSC). STORMONT CO.: Longue Sault Rapids, *Dore & Cody* 15087 (MSC). PARRY CO.: Island in French River, *Dewey* 39 (US). THUNDER BAY CO.: Sibley Peninsula, *Boivin* 2614 (MIN). WENTWORTH CO.: 1/2 mile from Lincoln Co. line, 2 miles from Winoma, *Gillis* 6317 (MSC). TIMISKAMING CO.: Dawson Point, Lake Timiskaming, *Morton & Le Page* 11687 (US). **Prince Edward Island.** Malpeque, *Fowler* 22104 (WIS). **Québec.** ARGENTEUIL CO.: Chatham Twp. Cushing, *Jenkins* 9036 (MSC). BELLECHASSE CO.: Beaumont, *Chabot & Verret* A-2204 (QUE). BERTHIER CO.: Berthier en Bas, *Rousseau* 22077 (GH). CHAMBLY CO.: Longueuil, *Marie-Victorin*, s.n. (ND). CHARLEVOIX CO.: Baie-des-Rochers, *Cayouette & Brassard* 5847 (QUE); Port-aux-Quilles (part of town of Cap-aux-corbeaux), *Cayouette & Barassard* 5846 (QUE). CHICOUTIMI CO.: Anse St. Jean, *Brassard*, s.n. (QUE). DEUX MONTAGNES CO.: Oka-sur-le-lac, *Cartier*, s.n. (QUE); La Trappe, Pinière Sablonneuse du lac, *Louis-Marie*, s.n. (OSC). GASPÉ CO.: Rivière Petit-Pabos, *Marie-Victorin, Jacques, & Rolland-Germain* 44919 (GH). GATINEAU CO.: Grand Remous, *Louis-Marie & Lamarre* 294 (GH). HEFFORD CO.: Granby, *Fabius* 373 (NY). HULL CO.: Hull, *Macoun* 427 (GH). IBERVILLE CO.: Iberville, *Cinq-Mars & Samoisette*, s.n. (QUE). LAC SAINT-JEAN CO.: Saint Gédéon, *Cayouette & Brisson* 6149 (QUE). LAVAL CO.: Saint Leonard, *Ricard & Boivin* 1020 (GH, MO); Mount Royal along railroad tracks, *Gillis* 3444 (MSC). MATAPEDIA CO.: Routhierville, *Cayouette & Cayouette* 6295 (QUE). MONTGOMERY CO.: Isle of Orleans, *Jack*, s.n. (A). MONTMORENCY CO.: Montmorency, *Marie-Victorin, Rolland-Germain, Raymond, & Champagne* 56889 (MSC). NAPIERVILLE CO.: Napierville, *Voss* 9085 (MSC). QUÉBEC CO.: Plaines d'Abraham, *Cinq-Mars & Barabé*, s.n. (QUE). ROBERVAL CO.: Pointe-Bleue, *Lalonde & Cayouette* 5691 (QUE). SAGUENAY CO.: Albert, *Cayouette* 840 (QUE); Petites Bergeronnes, *Cayouette & Brassard* 5863 (QUE). ST. JEAN CO.: St. Jean, *Cinq-Mars & Samoisette*, s.n. (QUE). **Saskatchewan.** South ridge of

Qu'Appelle River, *Shumovich, Selleck, & Gelleta* 67 (RM). Moon Lake near Saskatoon, *Boivin, Russel, & Breitung* 6709 (MSC).

Toxicodendron rydbergii is the most northerly ranging species in the Anacardiaceae. It is a taxon which is easily separated from related taxa by a number of constant characters, yet forms morphological intermediates on the fringes of its range where it apparently intergrades with neighboring taxa. At least eight species have been described by writers who apparently did not know its range of variation; at least three other taxa have been described which are probably intermediates between this species and other taxa, and represent populations from the edges of its range.

Prior to 1900 any specimens of this taxon were called by the names of other taxa — their collectors not being aware of any distinctions between them. It is possible that Linnaeus had such differences in mind in the Species Plantarum since he described three forms of poison-ivy, but his references are to the older literature and refer to names which cannot be typified.

The species is distinct from all other poison-ivy taxa in not producing aerial roots in the wild, thus always remaining a sub-shrub or, at best, a shrub of dimensions not more than several meters high. Its fruits tend to be larger and lighter in color than those of other taxa, its petioles always glabrous and usually quite long, and its leaflets very broad, often suborbicular. Because of the size and shape of the leaflets, they are difficult to press intact and therefore will often be folded along the midrib in herbarium specimens. In the field, this character is expressed by a spoon shape to the leaflets. The leaves are usually clustered near the top of the aerial stem, borne on petioles that are sometimes short, but more often than not, are more than one and a half times as long as the blade. Because the petiole length seems to be somewhat related to the degree of sunlight received by the plant, the length of petiole alone is not a definitive character; its glabrous nature is. The short pedicels bearing fruits larger than other members of the complex make the fruiting inflorescence much more compact

and tightly clustered than those of other taxa, hence the ability of the infructescence to stand erect.

In describing *Toxicodendron hesperium,* Greene distinguished the taxon by its wrinkled fruits, apparently unaware that unripe fruits of all members of this group become wrinkled upon drying. In regard to *T. pumilum* Greene, a different situation exists. *Toxicodendron pumilum* Kuntze (1891) is meant to refer to *Rhus pumila* Michx. (= *R. michauxii* Sargent) which is a homonym of *R. pumila* Meerb. *Toxicodendron pumilum* Greene therefore is also a homonym, having been published 14 years after Kuntze's name. Greene felt that this species was characterized by nodding inflorescences, but confused the issue by his statement describing the type: "In higher mountains of northern Arizona, . . . labeled *R. diversiloba,* though the plant, despite its inclining panicles, is strictly of the Atlantic type of the genus." The type is a collection from early in the growing season with new leaves barely opened and fruits dating from the preceding season.

In regard to *Toxicodendron punctatum* Greene, isotypes at NY and at US were annotated by Greene himself (after publication of this species) as *Rhus rydbergii*! Greene's description mentioned "tufts of hairs in and near axils of midveins" as a definitive character, but this trait does not characterize the type.

J. Lunell collected two forms in North Dakota, naming them *Toxicodendron fothergilloides* from the same locality which, even though given the same collection number, were collected two years apart. Barkley (1937) chose "type no. 1" as the type inasmuch as the Code provides only for a single specimen to serve as the nomenclatural type. It is a flowering specimen with a separate sprig of fruits attached to the sheet.

The range of this species extends throughout western United States roughly from the 100th meridian to the Great Basin and the Cascade Mountains. It is also the sole representative of the complex in North America found north of the 44th parallel of latitude. It is the taxon which inhabits the dunes of the Great Lakes and so follows the

shorelines of Lakes Michigan, Ontario, and Erie which extend south of the 44th parallel. A disjunct population is found on mountain crests in the central Appalachians from Pennsylvania, West Virginia, and Virginia. Except for the southern lobe of Ontario which bounds Lakes Huron, Erie, and Ontario, and for Nova Scotia, *Toxicodendron rydbergii* is the sole taxon of poison-ivy found in Canada from the Gaspé Peninsula to the east flank of the Cascade Mountains.

In garden plots at Michigan State University, where poison-ivy populations were grown experimentally, plants of *Toxicodendron rydbergii* maintained their distinctiveness especially in regard to the non-climbing habit. A specimen from the Davis Mountains of southwestern Texas, however, demonstrated a different behavior in a growth chamber. After several months at high relative humidity, aerial roots were produced. It appears that a response to moisture may induce aerial root formation even in this taxon, as a reversion to the stock from which it was derived. In the wild, it is this ability to produce roots which presumably permits the stolons to root upon stimulus by soil moisture, thus expanding a clone spatially.

Because of the apparent range limits at the 44th parallel in eastern United States, a study area was sought along a north-south river valley whose floodplains and terraces would likely be hospitable for the climbing forms to the south (*Toxicodendron radicans* subspp. *radicans* and *negundo*), yet a river valley which would cross the 44th parallel. The Connecticut River Valley, both in New Hampshire and Vermont, was explored. As I searched southward through New Hampshire, the first place where climbing poison-ivy was encountered was on a stream bank at the West Thornton-Woodstock city line in Grafton County at 44° N. This collection appears to be an intergrade between *T. rydbergii* and *T. radicans* subsp. *radicans*.

There is a cognate form of poison-ivy in Japan, also restricted north of the 44th parallel, and reported to be a sub-shrub. This taxon, named *Rhus rishiriensis* Nakai, is discussed under *Toxicodendron radicans* subsp. *orientale*,

and treated herein as an ecotype without being recognized nomenclaturally.

Plants of *Toxicodendron rydbergii* grow on sandy or rocky lakeshores, floodplains, river terraces, talus, precipices, railroad rights of way, and other ruderal sites, sand dunes, and cutover woods. It is frequently found with *Pteridium aquilinum* whereas most other poison-ivy taxa do not occur with bracken fern. It is seldom found in deep woods or old forests, having been shaded out, if it ever did occur there. When it is found on sand dunes, it is missing from the adjacent dune forest, being replaced, within their geographic ranges, by *T. radicans* subsp. *radicans* and subsp. *negundo*. In Nova Scotia and the Gaspé region it inhabits gypsum cliffs, slaty ledges, and the cobbly upper beach. It produces stolons that intertwine the chinks and crevices in stone walls of northern New England farms. Although often in wet places like rills, ravines, and near waterfalls, it is reported from sub-alpine rocks on Pike's Peak (Colorado). It is also reported as forming an "association" with *Shepherdia* in Dinosaur National Monument, Utah. In growth form, it is usually a sub-shrub, generally achieving no more stature than a meter. When it is undisturbed for several decades and the site conditions are favorable, it may reach two or more meters in height and be a genuine shrub. I have collected it under such conditions, from moist washes along the Columbia River in Washington and Oregon, and at the outlet of Montezuma Well in Yavapai County, Arizona.

Habitats for this taxon are many and varied. Because the taxon reproduces by rhizomes, it is difficult to assess the true abundance and ease of establishment of this species. The many stems appearing on a single site may all be of a single individual, or of several. It is not usually abundant, but may find its niche in the more mesic and better illuminated portions of the hemlock-white-pine-northern hardwoods association, the spruce-fir forest formation, the maple-basswood formation, or in a disturbed woods of pine, cherry, and red maple. In southern Ontario, *Toxicodendron rydbergii* inhabits woods of elm, oak, and ironwood *(Os-*

trya). It inhabits some of the more mesic habitats in the prairies and moist valleys in the Rocky Mountains. The ruderal nature of this plant permits invasion along roads, railroads, lakeshores, floodplains, fencerows, etc., where there are many weedy associates. It is probably safe to say that the plant's ecological amplitude is such that it will grow in situations too varied to characterize. Rather, the need for moisture and sunlight likely determines in large measure where it occurs.

6. **Toxicodendron toxicarium** (Salisb.) Gillis, comb. nov. Figs. 50, 52.

Rhus toxicodendron L., Sp. Pl. 1: 266. 1753. *Rhus toxicarium* Salisb. Prodr. 170. 1796. *Toxicodendron magnum* Bert. (sic) ex Steudel, Nom. Bot. 2: 694. 1841. *(nomen nudum)*. *Rhus toxicodendra* St. Lager, Ann. Soc. Bot. Lyon 7: 133. 1880. *Toxicodendron toxicodendron* (L.) Britton in Britton and Brown, Ill. Fl. U. S. 2: 484. 1913. Type: "Habitat in Virginia, Canada." (LINN 378.16, lectotype, specimen on left).

Rhus toxicodendron var. *quercifolium* Michx., Fl. Bor.-Am., 183. 1803. *Rhus quercifolia* (Michx.) Steudel (in synon.), Nom. Bot. 1: 689. 1821, non *R. quercifolia* Goeppert, Die Tertiäre von Schossnitz in Schlesien, 37. 1855. *Toxicodendron quercifolium* (Michx.) Greene, Leafl. Bot. Observ. Crit. 1: 127. 1905. Type: "Virginie et Carolines." (P, lectotype).

Rhus acutiloba Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 612. 1863. Type: *Berlandier* 2035, Mexico (actually Texas), (KW, lectotype, G-DC, GH, MO-1773755, isotypes).

Toxicodendron monticola Greene, Leafl. Bot. Observ. Crit. 1: 126. 1905. Type: *Albert Ruth* 356, Georgia, Lookout Mt., July 1898, (US-345540, holotype; ND-G, MO-1773749, NY, presumed isotypes).

Toxicodendron compactum Greene, Leafl. Bot. Observ. Crit. 1: 126. 1905. Type: *William Hunter*, s.n., Virginia, Carroll Co., Woodlawn, August 1899, (US-364942, holotype; GH, isotype).

Fig. 50. *Toxicodendron toxicarium.* Holotype of *T. monticola* Greene, *Ruth* 356.

Fig. 52. *Toxicodendron toxicarium.* Upper left: Lectotype of *Rhus toxicodendron* Linn. Right: *Lobadium aromaticum* (Ait.) Steudel, *P. Kalm.*

Rhus toxicodendron f. *elobata* Fernald, Rhodora 43: 598. 1941. Type: *S. S. Van Pelt*, s.n., Bridgeton, Cumberland Co., New Jersey, 1 1/2 miles s.e., by N. J. Central R.R., 20 July 1909. (GH, holotype).

Rhus toxicodendron f. *leiocarpa* Fernald, Rhodora 43: 599. 1941. Type: *M. L. Fernald & Bayard Long* 8347, dry open sandy pine and oak thickets near the county line, south of Jarratt, Sussex Co., Virginia, June 8, 1938, (GH, holotype, NY, US, isotypes).

Small shrub or subshrub with slender, pubescent branches and branching subterranean stolons. Leaflets often subcoriaceous, 3 (-5), ovate to oblong or oblong-obovate, lobate-dentate or lyrate, sinuate-pinnatifid with 3-7 rounded, blunt or rarely subacute lobes, occasionally just undulate; often more deeply lobed in male than in female clones; apex rounded, subacute or acuminate, base obtuse or cuneate. Petiole hispid or villous, 1.4-12.5 cm long, terminal leaflet blade 0.7-3.2 cm long. Leaves pilose, strigose, hirsute, or velutinous above, strigose, velutinous, or woolly below, often drying brown. Lateral leaflets inequilateral, subsessile or with petiolules up to 2.5 cm long; leaflets attached in palmate fashion when trifoliolate, pinnate when more than 3 leaflets. Inflorescence a lateral paniculate thyrse, up to 1 dm long; bracts deltoid to lanceolate, 0.6-10 mm long, 0.3-3 mm broad at the widest point, glabrate, ciliate, deciduous; sepals 5, deltoid-ovate, 1-2 mm long, 0.5-1.5 mm broad, glabrate; petals 5, cream to yellow-green, dark-veined, oblanceolate, glabrous, 2-4 mm long, 2-3 mm broad, reflexed in male, recurved in female, larger in male flowers than in female. Anthers lanceolate, 1-1.5 mm long, 0.5-1.1 mm broad, filaments linear-subulate, 1.0-1.8 mm long. Drupe hard, yellow-brown to tan, globose-reniform, sometimes depressed-globose, pubescent (rarely glabrate), exocarp becoming papery upon ripening and readily separating from the mesocarp; mesocarp striate in white waxy matrix; endocarp dun-colored, bony. Bark gray-brown to red-brown on new wood, becoming gray on older wood; leaf scars V- or U-shaped with several bundle scars; lenticels usually conspicuous; young branches villous. Buds stalked, naked,

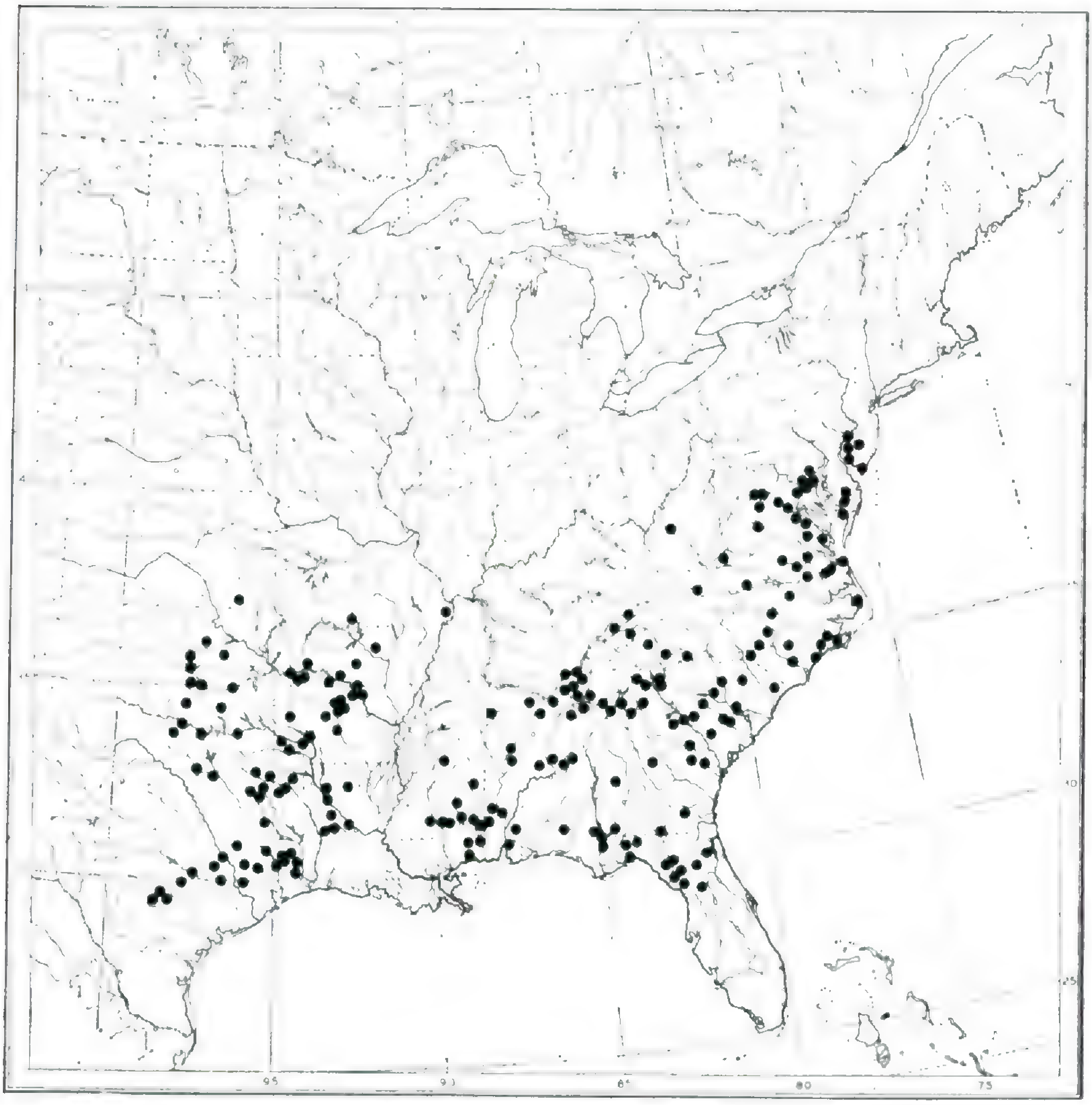


Fig. 51. Distribution of *Toxicodendron toxicarium.*

mucronate, brown, covered with a brown woolly pubescence. Autumn coloration red-bronze or brown.

Distribution: southeastern United States, New Jersey to Florida, west to Texas, north to southeastern Kansas. Common name: Eastern poison-oak. (Fig. 51.)

Representative specimens: UNITED STATES. **Alabama.** AUTAUGA CO.: Booth, *Gillis* 4530 (MSC). BALDWIN CO.: Loxley Research Plots, Stapleton, *Grelen* 5/59-46 (FLAS). BLOUNT CO.: *Eggert*, s.n. (MIN, MO, NY). CHOCTAW CO.: Bladonsprings, *Mohr*, s.n. (US). CLARK CO.: Jackson, *Gillis* 6021 (MSC). CLEBURNE CO.: north of Edwardsville, *Donahue* 249 (MSC); waterfall, Che-a-ha Mt., *Mohr*, s.n. (ALU). CULLMAN CO.: St. Bernard *Wolf*, s.n. (MO). DEKALB CO.: Ft. Payne, *Sherman* 298 (SMU). ELMORE CO., Wetumpka, *Gillis* 4524 (MSC). ESCAMBIA CO.:

Atmore, *Ahles* 7279 (ILL). HALE CO.: Payne Lake Recreation Area, Talledega National Forest, *Donahue* 245 (MSC). LEE CO.: Auburn, *Earle & Baker*, s.n. (F, KSC, MIN, MO, NY, RM); Auburn University, *Gillis* 4504 (MSC). MACON CO.: Tuskegee, *Gillis* 4509 (MSC). MARION CO., north of Hamilton, *Gillis* 6040 (MSC). TUSCALOOSA CO.: 3 miles south of Fosters, *Gillis* 6032 (MSC); Tuscaloosa, *Mohr* 231a (ALU). WASHINGTON CO.: 1 mile east of state line, *Gillis* 6012 (MSC). **Arkansas.** CLARK CO.: Arkadelphia, *Demaree* 17824 (A, MO, SMY); Graysonia, *Demaree* 21940 (A, ND-N, NY, SMU). CLEBURNE CO., Heber Springs, rim of Round Mt., *Demaree* 56274 (MSC). CONWAY CO., Petit Jean Mt., Morrilton, *Moore* 400 (SMU). DREW CO.: Ladelle, *Demaree* 22007 (A, MO); Monticello, *Demaree* 25409 (SMU). FAULKNER CO.: Cove Creek, *Demaree* 70 (MO); Greenbrier, *Gillis* 3777 (MSC). FRANKLIN CO.: north slope of Altus Hill, *Donahue* 225 (MSC). GARLAND CO.: Hot Springs, *Demaree* 17856 (MO, NY, SMU); Hot Springs, *Palmer* 24520 (A). GRAND PRAIRIE CO.: Hazen, *Wheeler* 78 (F). GRANT CO.: Poyen, *Demaree* 11052 (SMU). HEMPSTEAD CO.: Fulton, *Bush* 5677 (A, F, PH, MO). HOT SPRINGS CO.: Magnet Cove, Cook Mt., *Demaree* 19531 (MO, NY, SMU); Bismarck, *Demaree* 17405 (MO, WIS); Butterfield, *Demaree* 14519 (MO, NY); Malvern, *Palmer* 30361 (A). LAWRENCE CO.: Strawberry, *Demaree* 26212 (MU, TEX). LOGAN CO.: West Mt., *Palmer* 24520 (MO); east side of Magazine Mt., *Donahue* 227 (MSC). LONOKE CO.: Carlisle, *Demaree* 17570 (A, GH, MIN, MO, NY, SMU). MILLER CO.: Texarkana, *Demaree* 24476, (MO, NY, SMU). OUACHITA CO.: Camden, *Demaree* 16782 (A, MO, NY). PRAIRIE CO.: Hazen, *Palmer* 25052 (A, MIL). PULASKI CO.: Little Rock, *Palmer* 22943 (A). SALINE CO.: Bauxite, *Moore* 480198 (SMU). SCOTT CO.: 3 miles east of Y City, *Donahue* 229 (MSC). SEBASTIAN CO.: Mansfield, *Demaree* 18149 (SMU); Arkansas National Forest, *Palmer* 39315 (ND). SEIVER CO.: DeQueen, *Fassett & Watts* 19737 (GH, NY, WIS); Mineral, *Brinkley* 219 (F, TEX). YELL CO.: Dardanelle, *Demaree* 22769, 20055 (MIN, MO, NY, SMU). **Delaware.** SUSSEX CO.: Laurel, *Commons*, s.n. (GH, MO, NY). **District of Columbia:** Fort Totten, *Holm*, s.n. (MO). Woods near Sligo Creek, *Moffatt*, s.n. (ILL). Terra Cotta, *Holm*, s.n. (ILL, LCU, MO). Woodley Park, *Steele*, s.n. (A, F). Without locality, *Hitchcock* 12962 (US). **Florida.** ALACHUA CO.: Gainesville, *Gillis* 4315 (FLAS, MSC); oak-pine-hickory forest, University of Florida campus, *Wiggins & Wiggins* 19855 (FLAS); Wacahoota *West*, s.n. (FLAS). CLAY CO.: Goldhead Branch State Park, *West*, s.n. (FLAS). DIXIE CO.: 5.5 miles north of Oldtown, *Pasture Survey*, s.n. (FLAS). GADSDEN CO.: Aspalaga, *collector unknown* (MO). GILCHRIST CO.: Fort White, *Cooley & Brass* 8108 (SMU); *Wilcox, Martin, DeVall, & Arnold*, s.n. (FLAS). JACKSON CO.: west side of Apalachicola River, north of Victory Bridge, *Exploration Party* 1937 (FLAS); Marianna, *Godfrey* 60771 (MSC, SMU). JEFFERSON CO.: Wacissa and Capps, *Godfrey* 60640 (FSU, MSC, SMU). LAFAYETTE CO.: north of Mayo, *West & Arnold*, s.n.

(FLAS). LEON CO.: Tallahassee, *Godfrey* 53105 (FSU, GH, NY, SMU, VDB); Hammock, *Small, DeWinkeler, & Mosier*, s.n. (NY). LEVY CO.: locality unknown, *Hitchcock* 335 (F). LIBERTY CO.: pineland near Bristol, *West & Arnold*, s.n. (FLAS); 5.5 miles north of Bristol, *Godfrey & Henderson* 62875 (FLAS, FSU, MSC); MARION CO.: 2 miles south of Silver Springs *Gillis* 4487, 6867 (MSC). OKALOOSA CO.: Laurel Hill, *Godfrey* 61315 (FSU, MSC). SUWANEE CO.: locality unknown, *Hitchcock* 332 (F, MO); pineland 8 miles west of O'Brien, *West & Arnold*, s.n. (FLAS). WAKULLA CO.: Wakulla, *Godfrey* 60730 (MSC, NY, SMU). **Georgia.** BARTOW CO.: Cartersville, *Rhoades*, s.n. (WIS). BULLOCH CO.: locality unknown, *Harper* 948 (F, GH, MO). CLARKE CO.: Athens, *James*, s.n. (MSC). COBB CO.: Kenesaw Mt., *Rhoades*, s.n. (WIS). DADE CO.: Lookout Mt. *Ruth* 356 (MO, ND-G, US). DECATUR CO.: Bainbridge, *Gillis* 4500 (MSC). DEKALB CO.: Stone Mt., *Miller, Perry, Myers, & Boyel* 542 (GH); Lithonia, *Perry & Myers* 927 (GH). EMANUEL CO.: Swainsboro, *Gillis* 4966 (MSC). FLOYD CO.: Rome above Cossa River, *Demaree & Lipps* 50134 (MSC). GWINNETT CO.: Thompsons Mill, *Allard* 146 (US). HABERSHAM CO.: Currahee Mt., *Small*, s.n. (MSC, NY). HARALSON CO.: Tallapoosa, *Donahue* 251 (MSC). JEFFERSON CO.: locality unknown, *Hopkins*, s.n. (NY). LOWNDES CO.: 4 miles north of Clyattville, *Gillis* 6583 (MSC). MCDUFFIE CO.: near Sweetwater and Thomson, *Bartlett* 1702, 1703, 1704 (MICH, MSC). PEACH CO.: near Byron, 1.5 miles north of jct. I-75 and Ga-49, *Gillis* 6551 (MSC). RANDOLPH CO.: Shellman, *Sandlin*, s.n. (BLH). RICHMOND CO.: Augusta, *Sargent*, s.n. (A); Augusta, *Gillis* (MSC). WALTON CO.: Loganville, *Wiegand & Manning* 1862 (GH). WARE CO.: Waycross, *Gillis* 4975 (MSC). WHITFIELD CO.: Taylor's Ridge, *Wilson* 155 (E, F, GH). **Kansas.** CHAUTAQUA CO.: locality unknown, *Hitchcock*, s.n. (KSC). **Louisiana.** BIENVILLE PARISH: Castor, *Moore* 6407 (GH). JACKSON PARISH: Indian Village, *Moore & Marman* 5913 (GH). NATCHITOCHES PARISH: *Chopin* 7326 (A, F, MO). RAPIDES PARISH: Valentine Lake, *Thieret* 17923 (MSC). VERNON PARISH: LaCamp, *Donahue* 241 (MSC); 4 miles SE Ft. Polk, *Kral & Ricks* 16788 (FLAS). **Maryland.** ANN ARUNDEL CO.: Severn Run, *Reed* 29949 (FLAS, FSU, MO, NY, US). Baltimore, *Forman*, s.n. (NY). MONTGOMERY CO.: north end of Rock Creek Park, *Bartlett* 2243 (MICH, MSC). PRINCE GEORGES CO.: Clinton, *Holm*, s.n. (GH, KY, LCU). WICOMICO CO.: Salisbury, *Chickering*, s.n. (F, NY). WORCESTER CO.: Snow Hill, *Norton*, s.n. (MO). **Mississippi.** ATTALA CO.: locality unknown, *McDougall* 1615 (US). COVINGTON CO.: Collins, *Gillis* 6005 (MSC). GEORGE CO.: Lucedale, *Cooley, Pease, & Demaree* 3374 (GH). HARRISON CO.: DeSoto National Forest, *Diener* 905 (ILL). JEFFERSON DAVIS CO.: between Lucas and Prentiss, *Gillis* 6000 (MSC). JONES CO.: Laurel, *Teer* 64 (SMU, WIS). LAUDERDALE CO.: Meridian, *Rhoades*, s.n. (GH, RM). SMITH CO.: Marathon Lake, *Donahue* 243 (MSC). STONE CO.: McHenry, *DeMaree* 33379 (FSU, GH, SMU, VDB). WAYNE CO.: Beat Four School along

US-84, *Gillis* 6011 (MSC). **Missouri.** MISSISSIPPI CO.: Charleston, *Palmer & Steyermark* 41516 (A, MO). OZARK CO.: Tecumseh, *Palmer* 33025 (A, MO); Gainesville, Bald Jesse, *Palmer* 43891 (MO, NY); *Palmer* 33068 (A, MIN, NY). **New Jersey.** CAMDEN CO.: Cooper Creek, *Long* 18963 (GH); Somerdale, *Meredith,* s.n. (GH). CAPE MAY CO.: Goshen, *Gillis* 5631 (MSC); Locust Grove, West Medford Branch of railroad, *Long,* s.n. (MICH). CUMBERLAND CO.: Bridgeton, *Van Pelt,* s.n. (GH); Millville, *Gillis* 5634 (MSC). GLOUCESTER CO.: Woodbury, *Long,* s.n. (GH); Malaga, shore of Lake Malaga, *Gillis* 4044 (MSC). **North Carolina.** BLADEN CO.: Tackeel, AHLES 29161 (GH). BUNCOMBE CO.: Asheville, *Schneck,* s.n. (ILL). CARTERET CO.: Longleaf, *Gillis* 3883 (MSC). CUMBERLAND CO.: Fayetteville, *Miles,* s.n. (US); Cedar Creek, *Ahles & Hammond* 24447 (NY). DARE CO.: Manteo near old fort, Roanoke Island, *Churchill,* s.n. (MSC). DURHAM CO.: Nelson, *Gillis* 4030 (MSC). FRANKLIN CO.: Nash, *Ahles* 16514 (SMU). MOORE CO.: Carthage, *Fox, Godfrey & Campana* 1381 (FLAS, GH, SMU). ONSLOW CO.: Gum Branch, *Boyce & Moreland* 640 (GH). PENDER CO.: 4 miles south of Wallace, *Kral* 10091 (FSU). POLK CO.: Tryon, *Millsbaugh* 4060 (F). RICHMOND CO.: locality unknown, *Wiegand & Manning* 1861 (GH). **Oklahoma.** ATOKA CO.: 12 miles south of Atoka, *Hopkins & Nelson* 1103 (RM). CLEVELAND CO.: Norman, *Woodward* 92 (MO). CREEK CO.: Bristow, *Gillis* 5123 (MSC). GARVIN CO.: Davis, *Palmer* 57 (NY). LOGAN CO.: Guthrie, *Carleton,* s.n. (ILL). LOVE CO.: Hickory Creek north of Marietta, *Gillis* 5144 (MSC). OKLAHOMA CO.: Oklahoma City, *Campbell,* s.n. (MIN). PAYNE CO.: Stillwater, *Waugh* 124 (F, KSC). PITTSBURG CO.: McAlester, *Palmer* 6402 (A, F, MIN). POTTAWATOMIE CO.: St. Louis, *Faulkner* 66 (GH). **South Carolina.** AIKEN CO.: Mt. Pleasant, *Gillis* 4614 (MSC); north of Augusta, Ga., *Gillis* 4930 (MSC); Graniteville, *Eggert,* s.n. (MIN, MO); Aiken, *Harbison* 1159 (A, E). ANDERSON CO.: Anderson, *Davis* 1435 (US). BARNWELL CO.: Williston, *Palmer* 39870 (A, MO). CHEROKEE CO.: Draytonville Mt., ESE of Gaffney, *Ahles* 26988 (FLAS). CLARENDON CO.: Paxville, *Godfrey & Tryon* 1011 (GH, NY). DARLINGTON CO.: Darlington, *Rehder* 966 (A). GREENVILLE CO.: near Greenville, *Small,* s.n. (NY). HORRY CO.: locality unknown, *Weatherby & Griscom* 16583 (GH). KERSHAW CO.: Camden, *Palmer* 42394 (A, MO, NY). LEXINGTON CO.: Gaston, *Gillis* 4002 (MSC); Pleasant Hill, *Gillis* 4611 (MSC). OCONEE CO.: Tomassee, *House* 2051 (US). ORANGEBURG CO.: Eutawville, *Godfrey & Tryon* 829 (G, GH, MO, NY). PICKENS CO.: Clemson, *House* 3354 (NY). RICHLAND CO.: Columbia, BARTRAM, s.n. (NY); north of Columbia along highway 21, *Gillis* 4582 (MSC); Fort Jackson, *Gillis* 4014 (MSC). **Tennessee.** GRAINGER CO.: Rutledge, *Norton,* s.n. (ND-G). HAMILTON CO.: Chattanooga, *Churchill,* s.n. (GH); Lookout Mt., *Sharp & Hesler* 1060 (SMU). KNOX CO.: Knoxville, *Lamson-Scribner,* s.n. (US). SEVIER CO.: Sevierville, *Palmer* 42509 (A, MO). **Texas.** BASTROP CO.: Bastrop, *Lundell & Lundell* 10334 (F, NY, SMU); Bastrop

State Park, *Gillis* 3694 (MSC). BEXAR CO.: near Rio Medina, *Berlandier* 2035 (KW, G-DC, GH, MO). BOWIE CO.: 8.8 miles NNE of Sulphur River, *Donahue* 231 (MSC). BRAZOS CO.: 12 miles NE of Bryan, *Donahue* 234-A (MSC). BURLESON CO.: Somerville, *Shinners* 14694 (SMU). CALDWELL CO.: locality unknown, *McBryde*, s.n. (TEX). DALLAS CO.: Dallas, *Reverchon* 154, (A, F, GH, MO). GRAYSON CO.: Denison, *Reverchon*, s.n. (MIN, MO). HARDIN CO.: Kountze, *Demaree* 55416 (MSC). HARRIS CO.: Hickley, *Thuron*, s.n. (US). HARRISON CO.: Marshall, *Palmer* 5288 (A, MIN). HENDERSON CO.: NNE of Frankston, *Donahue* 232 (MSC). HOUSTON CO.: WNW of Ratcliff, Davy Crockett National Forest, *Donahue* 233 (MSC). JASPER CO.: Bouton Lake Recreation Area, Angelina National Forest, *Donahue* 240 (MSC). LAMAR CO.: Arthur City, *Demaree* 12006 (A). MONTAGUE CO.: St. Joe, *Shinners* 13272 (SMU). MONTGOMERY CO.: Conroe, *Palmer* 33331 (A, MO, NY). POLK CO.: Livingston, *Palmer* 5228 (A, F, MIN); NE of Camden, *Tharpe, Turner & Johnston* 54738 (TEX). RUSK CO.: Henderson, *Shinners* 14036 (SMU); Tatum, *Cory* 56464 (SMU). SMITH CO.: western Tyler, north of Pine Bluff Rd. *Cory* 56191 (F, NDA, SMU). TARRANT CO.: locality unknown, *Ruth* 550 (F, US). UPSHUR CO.: Big Sandy, *Shinners* 14380 (SMU). WALKER CO.: Huntsville, *Palmer* 12049 (A, MO). WALLER CO.: Hempstead, *Hall* 78 (F, ND-G, NY, MO). WILSON CO.: Ted Cover Road, *Cory* 55405 (SMU). WOOD CO.: Mineola, *Shinners* 14360 (SMU). COUNTY UNKNOWN: between Bejar and Trinidad Rivers, *collector unknown* (G-DC). **Virginia.** ARLINGTON CO.: Oakcrest, *Hotchkiss* 5861 (ND-G, NY); Naucks, *Steele*, s.n. (A). AUGUSTA CO.: locality unknown, *Caro* 466 (GH). CAROLINA CO.: Milford, *Fernald & Long* 7518 (GH, PH). CARROLL CO.: Woodlawn, *Hunter*, s.n. (GH, US). CULPEPPER CO.: Buzzard Mt., *Allard* 20851 (US). DINWIDDIE CO.: Carson, *Fernald, Long, & Smart* 5834 (GH, PH); Petersburg, *Fernald & Long* 8346 (GH, MO, NY, PH). FAIRFAX CO.: Great Falls, *Bartlett* 1784 (MICH, MSC, SMU). FAUQUIER CO.: western slope of Bull Run Mt., *Allard* 10006 (GH, US). GREENSVILLE CO.: Orion, *Fernald & Long* 13675 (GH, PH, US). NANSEMOND CO.: South Quay, *Fernald & Long* 10322 (GH, PH, US). PAGE CO.: Kimball, *Miller*, s.n. (US). PRINCE EDWARD CO.: Farmville, *Fosberg* 15541 (GH). PRINCESS ANNE CO.: Cape Henry, *Egler* 40-151 (NY); Richmond, University of Richmond Campus, *Clarke* 996 (GH); *Churchill*, s.n. (GH). ROANOKE CO.: Hanging Rock, *Wood* 3094 (GH). SHENANDOAH CO.: Massanutten Mt., *Allard* 6618 (F, MO, NY, US); South of Elizabeth Furnace Forest Camp, *Chrysler* 3027 (CHRB). SPOTSYLVANIA CO.: Fredericksburg, *Iltis* 220 (SMU). SUSSEX CO.: Jarrett, *Fernald & Long* 8347 (GH, NY, US); Williamsburg, *Grimes* 3667 (GH). **West Virginia.** KANAWHA CO.: Pine Top Ridge, Loudon District, *Fletcher*, s.n. (MSC).

The Tournefort name *Toxicodendron*, which has been used for this generic segregate of *Rhus*, was chosen by

Linnaeus as the specific epithet for Eastern poison-oak. Tournefort (1700), Barrelier (1714), and Gronovius (1743) may have had this plant in mind when they described *Toxicodendron triphyllum folio sinuato pubescente*, for its leaves are characteristically sinuate or lobed and pubescent. Linnaeus included this polynomial phrase in synonymy under his *Rhus toxicodendron*. However, no specimens representing this species which were probably seen by these early authors appear to be extant to confirm their identity. Furthermore, in the Michaux Herbarium, there is a specimen labeled with this same polynomial phrase that is *T. rydbergii*. It is with Michaux that much of the nomenclatural confusion begins, as mentioned earlier. The point to be made herein is that authors before and after Linnaeus have had different taxa in mind in their use of *Rhus toxicodendron* as a name, or polynomial phrases associated with it. Typification of the Linnaean name is therefore exceedingly important.

The lectotype sheet at LINN (sheet 378.16 Fig. 52) bears two plants; the one on the left represents the taxon here recognized; the other is aromatic sumac [*Rhus aromatica* Aiton = *Lobadium aromaticum* (Ait.) Raf. ex Steudel]. The specimen on the left, then, is chosen as the lectotype of *Rhus toxicodendron*. This species name has been used indiscriminately for poison-oak (both *Toxicodendron diversilobum* and *T. toxicarium* and poison-ivy (*T. radicans* and *T. rydbergii*). Of the infraspecific names proposed for various members of the complex using *Rhus toxicodendron* as a base, one has been applied to Western poison-oak, three to Eastern poison-oak, and twelve to poison-ivy!

Many persons have used the name *Rhus toxicodendron* in preference to *R. radicans* because it is perhaps more euphonious and more suggestive of the toxic nature of the plant. A rough count of herbarium specimens examined shows that it has been used more frequently (and carelessly) than any other binomial with reference to either poison-ivy or poison-oak. It was not even spelled in full by Linnaeus until the publication of Systema Naturae, ed.

11 (1760). A good discussion of the orthography is given in Fernald (1941, pp. 597-599).

Michaux (1803) published the epithet *quercifolium* without rank indicated, but variety implied. It was Eaton (1818) who designated the rank as *Rhus toxicodendron* var. *quercifolium*. Steudel (1871, p. 689) made the combination *R. quercifolia*, but lists it in synonymy and should not, according to the Code (Lanjouw *et al.*, 1966), be cited as author of the combination. Robinson and Fernald (1908) made the combination legitimately, although they attribute it to Steudel. In the meantime, however, this combination was validly published as a fossil species, *Rhus quercifolia* Goeppert from the Tertiary of Bohemia (Goeppert, 1855).

To give some idea of the nomenclatural "mess" (to quote Fernald's well-chosen word regarding this complex) involving the epithets *toxicodendron* and *radicans*, some combinations are listed below. Where their true identity can be correlated with a known species, the names are listed in the appropriate synonymy in the taxonomic treatment; where they are not, such names are listed in a group of doubtful species.

Rhus toxicodendron L. (1753, p. 266)

R. radicans var. *toxicodendron* Persoon (1805, p. 325)

Rhus-Toxicodendron radicans Marshall (1785, p. 131)

Rhus-Toxicodendron toxicodendron Marshall (1785, p. 131)

R. toxicodendron var. *radicans* Eaton (1818, p. 400)

R. toxicodendron forma *radicans* McNair (1925, p. 68)

R. toxicodendron subsp. *radicans* Clausen (1949, p. 8)

Toxicodendron toxicodendron (L.) Britton (1913, p. 484)

All of these have been cited by other authors. Also, *Rhus toxicodendron radicans* (without rank specified) has been attributed in the literature to Torrey, Dippel, Miquel, and to "Farr." (sic) (Dodge, 1911), and *R. toxicodendron* attributed both to Linnaeus and to Small by McNair (1925). McNair *(loc. cit.)* also mentions a var. *typica* which has no nomenclatural status according to the Code.

With respect to *Toxicodendron vulgare* Miller (Gard. Dict., ed. 8, Art. *Toxicodendron*, No. 1, 1768), confusion

of a different sort pertains. It was not Miller's custom to cite Linnaean binomials when transferring species to other genera, or when providing new epithets for them, but to give a reference at the beginning of the account which established a connection with the earlier literature. He used Linnaean epithets where appropriate; in other cases, he used pre-Linnaean names, citing the source of the original publication. A synonym which Miller (and others) frequently cited as "*Toxicodendron triphyllum folio sinuato pubescente*" (Tournefort, Inst. Rei, Herb. 611) links the name *T. vulgare* Mill. with *Rhus toxicodendron* L., being a polynomial phrase shared in the two descriptions. The lectotype of the Linnaean name accordingly typifies the name substituted for it by Miller. This is the species which herein is called *T. toxicarium.*

Should not the epithet *vulgare* of Miller (1768) have priority over *toxicarium* first applied as a species epithet by Salisbury (1796)? It probably would if Miller's Latin and English diagnoses accurately described Eastern poison-oak, but they do not. He described the "foliolis" as: "obcordatis, glabris, integerrimis," and adds further, "caule radicante." Still further, he continues, "with roundish, heart-shaped, smooth, entire, trifoliate (sic) leaves, and a stalk putting out roots." Eastern poison-oak has leaflets which are not obcordate, not glabrous, and are lobed, not entire. The stem is not climbing; the stalk never produces aerial roots. Inasmuch as the species which Miller named as *Toxicodendron vulgare* is too inaccurately described to be Eastern poison-oak, even though indirectly linked with that species in the literature (thus satisfying Art. 32 of the Code), this binomial must be rejected under Art. 69 of the Code.

A specimen at Kiev representing *Rhus acutiloba* Turcz, was collected in Texas by Berlandier. At the time of Berlandier's explorations in Texas (1827-1830), this region was part of Mexico, hence the word "Mexico" on the label. This taxon is not found in present-day Mexico. It was presumably collected in Southeastern Texas (McKelvey, 1955). An isotype at the Gray Herbarium completes

the story: the specimen was collected near the Medina River in July 1829. According to McKelvey *(loc. cit.)*, this would have been 15-16 July, just south of present-day San Antonio in Bexar County. Another specimen cited by Turczaninov (at KW) is *Mathes* 160 from Taylor County, Texas. This is a mixed collection; the two large specimens on the sheet are *Toxicodendron radicans* subsp. *verrucosum*, but the small sprig in the upper right corner is *T. toxicarium*.

There are many populations of Eastern poison-oak in which leaflets of the male clones differ from the leaflets of female clones. Most often, the leaflets on male plants are more deeply lobed than those of female clones. In fact, some of the leaflets in female plants may be elobate or with undulating leaflet margins. Fernald named the form *Rhus toxicodendron* f. *elobata*, separating it simply on the basis of sexually dimorphic characters, apparently unaware that this was the case.

In collecting material which later became the type for *Toxicodendron monticola*, Ruth apparently numbered specimens, rather than gatherings. Hence, the specimens at ND-G, NY, and MO are presumed isotypes. Greene did not clearly cite a type specimen, but indicated *Ruth* 356 as representative. This specimen is therefore designated lectotype. Because of the uncertainty with which Greene deals with *Percy Wilson* 155 from Taylor's Ridge, Georgia, this specimen is not considered a syntype. Greene's diagnosis described the leaves as bright green, yet the leaves of the type have dried brown, and he probably saw it after the plant was dried.

Often used in connection with this species is the epithet *pubescens*. Philip Miller originally published the name *Toxicodendron pubescens* (Gard. Dict., ed. 8, Art. *Toxicodendron*, No. 2, 1768). His description fits *T. toxicarium* which has pubescent leaves and fruits, but not to the exclusion of all other taxa. Apparently no specimen upon which this name could be based is extant. Thunberg (1794) published the epithet again, this time as *Rhus pubescens* for a plant from the Cape of Good Hope, not a member of the poison-ivy complex, but a *Rhus* sect. *Thezera*. *Rhus pubescens* Engelmann ex Engler in DC. (1883) was a new name

(and a homonym) published for a plant that is likely to be *T. radicans* subsp. *radicans*, which has pubescent fruits. Type specimens — designated or implied — are known for none of these. In 1900, Farwell published another *Rhus pubescens*, indicating that he was transferring the name from Miller, although, judging from the region covered by his work (Michigan), not to represent the same species. As was his custom, he named a "type specimen" (sic) which is at BLH with a duplicate at ND-G. Farwell's "type" is *T. radicans* subsp. *negundo*.

The formal epithet of *R. toxicodendron* f. *leiocarpa* means "smooth-fruited," but the holotype has pubescent fruits (although the sheet bears the notation "glabr. fr."); furthermore, the fruits are immature and shriveled, not readily demonstrating any papillose condition. The glabrate or glabrous nature of the fruit might be due in part to their immaturity (their having been collected early in June) and therefore should not be considered diagnostic. The holotype has some aborted ovary tissue such as that described for New Jersey poison-ivy by Gillis (1960). Isotypes at NY and US were annotated by Fernald as a form of *Rhus radicans* (sic) in error.

Toxicodendron toxicarium clearly is the most misunderstood species in the poison-ivy complex. The common name, poison-oak, is related to the typical leaflet shape, which resembles the leaf of a species of the white oak group. This common name has been used in different senses by physicians, Boy Scouts, extension agents, botanists, and others until it has lost its meaning. Most often it is used to represent *T. rydbergii* or a shrubby or arborescent form of *T. radicans*. The plant is seldom encountered in the wild by non-botanists because of its habitat requirements. It is practically restricted to low-nutrient sands of the Atlantic and Gulf Coastal Plains, generally in association with scrub-oak and pine woods (sandhills vegetation) that have little economic value. It is seldom abundant. Although it produces aerial stems from its stolons, it does so at far greater intervals than its counterparts *T. radicans* or *T.*

diversilobum. In habit, it resembles the sub-shrub *T. rydbergii* more than any other member of the complex.

This plant is found most often in scrub-oak and pine woodland savanna that has an understory of ericaceous shrubs and bunch grasses, chiefly *Aristida, Stipa,* and *Andropogon,* characteristically found in the sandhills of the Carolinas. In Oklahoma, where the same general vegetation type, minus the pine, may be found, *Toxicodendron toxicarium* occurs also. The soils in which it grows are most often coarse sands, generally low in calcium, magnesium, and potassium. In fact, the Lakewood and Norfolk sands in which it has been found most often are the soils with the lowest nutrient values of any along the Atlantic Seaboard. For this reason, its requirements are such that it seldom occurs in the same association with any other taxa of the complex, all of which generally prefer richer soils.

In a very few instances, putative hybrids between *Toxicodendron toxicarium* and *T. radicans* subspp. have been found. The former is contained within the combined ranges of *T. radicans* subsp. *radicans, pubens,* and *verrucosum.* It might be expected, given the environment intermediate between that restricted one required by *T. toxicarium* and the rather broad one permitted by subspecies of *T. radicans,* that some gene interchange might take place. In the field, although such situations are comparatively rare, several have been found. One from Bastrop County, Texas, suggests crossing between *T. radicans* subsp. *verrucosum* and *T. toxicarium* in a region where both are abundant. Several collections have been made in New Jersey, Georgia, and South Carolina which seem to be intermediate between *T. toxicarium* and *T. radicans* subsp. *radicans.* Other putative hybrids have been seen among herbarium specimens. A more complete discussion of putative hybrids is discussed in the section on "Hybrids, Crosses, and Intergrades."

The relative rarity of intermediate forms throughout the southeastern states where both of these species are frequent, if not common, has been a guiding factor in recognizing them as distinct species. Although hybridizing can appar-

ently occur, it is not an important factor in the genetics of these populations.

Part of the difficulty in recognizing the species *Toxicodendron toxicarium* in the field is the degree of lobation of the leaflets. Leaflet margins may be undulate or almost entire varying through degrees of lobing to crenate or deeply lobed. Often, as mentioned before, one sex may have leaflets more distinctly lobed than the other, all within the same population. It is usually the male which has more deeply lobed leaflets than the female, but the converse may also be true. The most significant morphological features, then, are the pubescent nature of the leaves and fruits, the non-climbing habit, and the rather impoverished habitat.

In published keys, one finds that some previous workers have considered thickness of the leaves to be a major factor separating *T. toxicarium* from related taxa. From anatomical sections, I have measured a number of leaves of various of these species, and found no consistent difference. The leaves of *T. toxicarium* are also described as leathery. They perhaps have a slightly thicker cuticle, a possible evolutionary result of the plant's being found on drier sites than is poison-ivy, but otherwise, this character is variable. The thickness or leathery nature of the leaflets is hardly conducive to field determination in such a dermatitis-producing plant!

HYBRIDS, CROSSES, AND INTERGRADES

A study of naturally-occurring suspected hybrids found in the field was made, and an attempt was made to produce hybrids artificially. Difficulty in obtaining germination precluded the latter's being wholly successful, but nevertheless some data of significance were accumulated. Suspected natural hybrids have been found and are herein described along with ecological and geographical considerations.

FIELD STUDIES

Because several subspecies of *Toxicodendron radicans* and *T. toxicarium* overlap in range, a search was made for natural hybrids between them. As will be discussed later,

these two species rarely exist in the same vegetation association or soil type. Even on the few occasions where one finds them occurring together, there is a paucity of intermediate forms. Several of these associations were investigated in detail.

In the San Felasco area of Alachua County, Florida, there is an extensive tract (T. 9S., R. 19 E., Sec. 21) of mixed community of hammock and sandhills vegetation (Monk, 1960), where both *Toxicodendron radicans* subsp. *radicans* and *T. toxicarium* grow abundantly side by side. Despite intensive searching, I was unable to find any intermediate forms between these two readily distinguishable species. Both flower at the same time (early April) and are pollinated by honey bees, although few female flowers of *T. radicans* were found in the population.

In a study area north of Columbia, Richland County, South Carolina, in a narrow band of overlap between poison-ivy and Eastern poison-oak (c. 10 meters), there was only one individual with intermediate characters found (*Gillis* 4582). This individual has some of the leaflet shape, notching and color of *Toxicodendron radicans* subsp. *radicans*, but the pubescence and growth form (sub-shrub) of *T. toxicarium*. The cited specimen is a female in flower.

In another study area in Bastrop County, Texas, between Beuscher and Bastrop State Parks, one finds pockets of *Toxicodendron radicans* subsp. *verrucosum* and others of *T. toxicarium*, the latter growing on the poorer soils. Only one suspected hybrid was discovered, a sterile specimen which possessed the leaf pubescence of *T. toxicarium* but the climbing habit of *T. radicans* subsp. *verrucosum* (*Gillis* 5167). The lobing is intermediate between the rounded lobes of *T. toxicarium* and spreading, sharp lobes of *T. radicans* subsp. *verrucosum*.

A suspected hybrid clone (between *Toxicodendron toxicarium* and *T. radicans* subsp. *radicans*) was found in Jefferson County, Georgia, in a loblolly pine and sassafras woods (*Gillis* 4965). It shared with poison-ivy the climbing habit and the tendency to have entire leaflet margins, but had the pubescence of Eastern poison-oak.

Artificial crosses were made between *Toxicodendron radicans* subsp. *radicans* and *T. toxicarium* in Alachua County, Florida, and in Richland County, South Carolina, in the areas mentioned above during the spring of 1961. Because of a dearth of female flowering poison-ivy plants, reciprocal crosses were not possible in the Florida experimental plots. Crosses which were made in South Carolina were each replicated in three inflorescences and bagged to prevent contamination by insects. Pollen was transferred from anther to stigma by means of a loblolly pine needle. The population of Eastern poison-oak had sexually dimorphic leaves, so that the male clones could be distinguished from the females even when only unopened flowers were present. Flowers which had not yet opened, but for which flowering appeared imminent, were chosen exclusively. Results were considered successful if fruits were produced.

Where *Toxicodendron radicans* was the female parent, the fruits were small (3.5-4.0 mm broad), whereas the fruits were more typically the size of *T. toxicarium* fruits (5.5-6.5 mm broad) where this plant was the female parent. The hybrid seeds were indistinguishable from normal seeds whose parentage represents but a single species. It is to be noted that no fruits at all developed from unpollinated controls, thus making it unlikely (but not impossible) that apomixis might be taking place. Germination of the hybrid seeds was attempted, but no seedlings resulted. But then, I have succeeded in germinating only two seeds of *T. toxicarium* in trials numbering more than 200 seeds of pure parentage.

Results, as shown in Table 5, suggest that there is no apparent difference in percentage of successful crosses between open-pollinated flowers and artificial hybrids, at least not in the South Carolina series. In the Florida trials, however, the number of interspecific crosses producing fruits was half that of open-pollinated poison-ivy flowers.

In the gorge of the Columbia River between Oregon and Washington, there is overlap in range of *Toxicodendron diversilobum* from the west and *T. rydbergii* from the east. In studies made in late summer and early autumn of 1960

TABLE 5. INTERSPECIFIC CROSSES BETWEEN TOXICODENDRON RADICANS SUBSP. RADICANS AND T. TOXICARIUM. CROSSES WERE MADE IN ALACHUA COUNTY, FLORIDA, ON 6 APRIL 1961 (lettered) AND IN RICHLAND COUNTY, SOUTH CAROLINA ON 12 MAY 1961 (numbered). RESULTS WERE GATHERED IN EARLY SEPTEMBER 1961 AT BOTH SITES

Cross Number	Replication	Male Parent	Female Parent	Number of Flowers Pollinated	Number of Resulting Fruits	Percentage Successful Crosses	Mean Per Cent
Y	A	*T. toxicarium*	*T. radicans*	38	21	55	
	B			41	16	39	41
	C			20	6	30	
Z	A	*T. radicans*	*T. radicans*	56	45	80	
	B			63	51	84	82
1	A	*T. toxicarium*[1]	*T. toxicarium*	22	6	27	
	B			10	7	70	52
	C			32	19	59	
2	A	*T. toxicarium*[2]	*T. toxicarium*	18	10	55	
	B			20	10	50	57
	C			50	32	64	

3	A	*T. radicans*	*T. toxicarium*	34	15	44	58
	B			41	22	54	
	C			20	16	75	
4	A	open-pollinated	*T. toxicarium*	44	23	52	47
	B			55	16	29	
	C			34	20	60	
5	A	unpollinated	*T. toxicarium*	38	0	0	0
	B			27	0	0	
	C			42	0	0	

[1]Source of pollen was from different populations.
[2]Source of pollen was from same population.

and 1962, the populations of these two were examined and samples collected from along the two sides of the gorge. The zone of overlap produced an apparent introgressive series between these two taxa. The zone of apparent hybridization extends in Washington from the confluence of the Klickitat and the Columbia Rivers eastward 43 miles to the vicinity of the John Day Dam, and in Oregon from the Hood River eastward 23 miles to the vicinity of The Dalles. There is evidence that this zone of overlap is restricted to the gorge because populations immediately south of Hood River appear to be genetically pure *T. diversilobum* (*Gillis* 5231 from 2 miles south of Hood River city limits). Furthermore, neither taxon grows above 1275 meters in the Cascades which rise to the north and south of the gorge.

In a roadside park at the confluence of the Klickitat and Columbia Rivers there is a large shrub of *Toxicodendron diversilobum* surrounded by a clone of suspected hybrids. These populations were seen late enough in the season to demonstrate their autumn coloration. The difference between the two taxa was therefore striking. From this location, each population of the taxa was studied as I collected eastward through the gorge. Each population in the zone of overlap was sampled until populations appeared to be fairly constant as typical *T. rydbergii.* It is in the same region that flowering and fruiting material were collected by Suksdorf in the late 1800's. The latter collections were the basis for two new species names by Greene (1905). Presumably these collections represent hybrid populations.

Eastward through the gorge from Hood River in Oregon or from the Klickitat River in Washington, fruits of the *Toxicodendron* species become smaller, less pubescent, more nearly globose, and on shorter pedicels. The inflorescence becomes more compact and more erect than pendent. The leaves progressively become less crowded at the summits of branches, lose the pubescence of the petioles, assume a more yellow-orange (less red-brown) autumn coloration, lose the tendency for the peculiar mottling of the dried leaves of *T. diversilobum* and tend to have the broadest

part of the leaflet below the midpoint, becoming ovate rather than elliptic. (Fig. 53.)

HERBARIUM STUDIES

In the course of examination of populations in the field plus examination of herbarium specimens, I have determined a number of these to be intergrades between taxa. In several cases, the situation indicates that these intergrades are very likely hybrids. In others, the nature of the intergrades is less certain, possibly examples of incomplete divergence among taxa. *Toxicodendron diversilobum* and *T. rydbergii*, for example, occupy completely separate ranges except for a zone of overlap in the Columbia River gorge, as mentioned above. It seems justified to interpret the intergrades in the gorge as putative hybrids. The rather blurred separation between *T. radicans* subsp. *negundo* and subsp. *radicans* in the Allegheny Mountains may be interpreted as hybridization, but, on the other hand, may also be looked upon as intergrading due to current speciation. The Alleghenies are not a completely effective barrier to gene exchange between subsp. *radicans* to the east and subsp. *negundo* to the west. They are treated here as hybrids, but the case of incipient speciation cannot be ruled out.

HYBRIDS OF SUBSPECIES OF T. RADICANS

Toxicodendron radicans subsp. **barkleyi** × subsp. **divaricatum.** Table 6.

The two Mexican subspecies of poison-ivy are not abundant in comparison with taxa found farther north. It is not surprising therefore that apparent intergrades between the two taxa are scarce. Only a few populations from the trans-Mexico volcanic belt or an extension of this mountain region seem to show traits intermediate between the two parental types. Such populations have been found in Jalisco, Guerrero, the Distrito Federal, Michoacan, and Oaxaca. (Fig. 55.) Characters which have been used to demonstrate the suspected hybrid nature of the populations are few. They are listed in Table 6.

It may be noted from Fig. 55 that these two subspecies

TABLE 6. CHARACTERS OF PARENT TOXICODENDRON RADICANS SUBSP. BARKLEYI, SUBSP. DIVARICATUM, AND OF THEIR PUTATIVE HYBRID OFFSPRING

Toxicodendron radicans subsp. *divaricatum*	Putative Hybrid	*T. radicans* subsp. *barkleyi*
Lower leaflet surface glabrous or with scattered erect strigose trichomes	Lower leaflet surface with scattered pubescence; essentially prostrate pilose hairs	Lower leaflet surface pilose to velutinous
Upper leaflet surface glabrous	Upper leaflet surface glabrate or with scattered hairs	Upper leaflet surface pubescent
Fruits usually glabrous, pubescent only in northern end of range	Fruits with scattered pubescence or nearly glabrous	Fruits always glabrous

appear to be sympatric in several regions. The concept of sympatric subspecies is an anathema to some taxonomists or evolutionists, because, by definition, subspecies have distinct geographical ranges. The Mexican populations of poison-ivy, however, bring to the fore some possible explanations for this phenomenon. One possibility is that the two subspecies evolved in separate regions, separated from one another by any of the traditional barriers to gene flow. Then, in relatively recent times, perhaps assisted by the activities of man, the two have expanded their ranges to overlap. Thus, only recently have they become sympatric and share genes. Another possibility is that they are not strictly sympatric in that they do not occupy the same communities as do, for example, *Acer nigrum* and *A. saccharum* in eastern North America. There has been no location found where they are growing close to one another. It is, then, their gross ranges which overlap, but not the refined patterns too small to show on a standard political map; that is to say, they are ecologically different, occupying the same overall range, but not the same communities.

A third possibility, not likely to be valid here, is that the two subspecies are just now speciating and exist relatively close together only as relicts of populations which existed prior to the erection of a barrier to gene flow. As interpreted herein, the two subspecies under consideration here were not derived from one another, but both have their closest relatives farther to the north of Mexico. A fourth possibility is also unlikely in this case, i.e., that either or both of the subspecies is apomictic and unable to share genetic information, yet have come to occupy portions of the same range.

Representative specimens: MEXICO. **Guerrero:** Barranca, Mina, *Hinton* 9488 (MICH, NY). **Jalisco:** Nevado de Colima, *Beaman* 2388 (MSC); Sierra del Halo, lumber road leaving Colima Highway, 7 miles SSW of Tecalitlan toward San Isidro, 2000 m., *McVaugh* 16229 (MICH). **Michoacan:** east of Morelia between Rio del Salto and La Polvilla, *King & Soderstrom* 5082 (MICH, SMU). **Nayarit:** Mountains 9 miles south of Compostela, heavily forested stream valley in oak zone, 1000-1200 m., *McVaugh* 16484 (MICH). **Oaxaca:** Reyes, *Nelson* 1789 (GH, US).

Toxicodendron radicans subsp. **negundo** × subsp. **pubens.** Table 7.

Toxicodendron radicans subsp. **pubens** × subsp. **radicans.** Table 7.

Considerable taxonomic difficulties are encountered in the region of overlap where *Toxicodendron radicans* subsp. *pubens,* subsp. *radicans,* and subsp. *negundo* intergrade. The number of specimens available for study which combine characters of these taxa is numerous, but not enough specimens are available from the most significant area, i.e., the second and third tiers of counties west of the Mississippi River in northern Louisiana, southern Missouri, and the intervening region of Arkansas. Perhaps it is due to active divergence among the taxa. More likely this large-scale variation is attributable to three-way hybridization among the taxa.

This region of the foothills of the Ozarks represents the western edge of the range of subsp. *radicans,* the northern edge of the range of subsp. *pubens,* and the southern edge of the range of subsp. *negundo.* No conclusions other than the probability of hybridization among these subspecies seem to be warranted at this time. Further field work in this area is desirable for resolution of the true nature of these populations. It is possible that the region in question is the center of diversity of a rapidly evolving species, but more likely a region which the three subspecies have been invading for a considerable period of time, perhaps since the Pleistocene.

For the time being, specimens from this region have been classified by the combination of several key characters. Pubescent fruits and tufts of hairs in the vein axils on the lower surface of the leaves have been interpreted as indicative of the presence of genes of subsp. *radicans.* The presence of dense, erect hairs in the interveinal area on the lower surface of the leaves is interpreted as indicative of the presence of genes of subsp. *pubens.* The presence of appressed hairs on the lower leaflet surface is indicative of the presence of genes of subsp. *negundo.* These clusters of

TABLE 7. CHARACTER CLUSTERS REPRESENTED IN VARIOUS POPULATIONS OF TOXICODENDRON RADICANS IN THE OZARKIAN REGION

subsp. *radicans*	subsp. *negundo*	subsp. *pubens*	subsp. *radicans* × *pubens*	subsp. *pubens* × *negundo*
Fruits pubescent	Fruits glabrous	Fruits glabrous	Fruits somewhat pubescent	Fruits glabrous
Tufts of hairs in vein axils present	Tufts of hairs absent	Tufts of hairs absent	Tufts of hairs present	Tufts of hairs absent
Hairs on lower leaf surface scattered	Hairs on lower leaf surface scattered	Hairs on lower leaf surface dense	Hairs on lower leaf surface dense	Hairs on lower leaf surface dense
Pubescence appressed	Pubescence appressed	Pubescence erect	Pubescence mixed appressed and erect	Pubescence mixed appressed and erect
Leaflets mostly entire	Leaflets mostly notched	Leaflets all notched or serrate	Some leaflets notched; some entire or subentire	Leaflets all notched or serrate
Leaflets ovate to lanceolate	Leaflets ovate	Leaflets broadly ovate	Leaflets broadly ovate	Leaflets broadly ovate

characters and the taxa they represent are shown in Table 7.

Toxicodendron radicans subsp. *negundo* × subsp. *pubens.*

Representative specimens: UNITED STATES. **Arkansas.** BENTON CO.: Twin Mountain, *Demaree* 4579 (F, MO, WIS). FULTON CO.: Salem, *Demaree* 26305 (SMU). WASHINGTON CO.: Lake Weddington Recreation Area, *Donahue* 224 (MSC). **Iowa.** POTTAWATTAMIE CO.: Council Bluffs, *Demaree* 23666 (MO, SMU). **Kansas.** POTTAWATOMIE CO.: St. George, *Kellerman*, s.n. (KSC). SUMNER CO.: Geuda, *Gassler*, s.n. (MIN). **Missouri.** OREGON CO.: Pine, on country road J., *Donahue* 219 (MSC). OZARK CO.: Tecumseh, *Palmer* 32912 (A, MO, NY).

Toxicodendron radicans subsp. *pubens* × subsp. *radicans.*

Representative specimens: UNITED STATES. **Arkansas.** CONWAY CO.: Morrillton, Petit Jean State Park, *Demaree* 22801, 36876 (GH, MO, NY, SMU). CRAIGHEAD CO.: Lake City, *Demaree* 7218 (GH, SMU, TEX, WIS). GARLAND CO.: Hot Springs *Demaree* 22056 (A, MIN, MO, NY); Hot Springs, *Palmer* 23098 (A, MIN). HEMPSTEAD CO.: Fulton, *Bush* 5647 (A, US). MONTGOMERY CO.: Norman, *Demaree* 9563 (GH, MO, SMU). POPE CO.: Hector, *Merrill* 52 (*A*, MIN, NY); Nogo, *Merrill* 332 (MIN, MO). PULASKI CO.: Little Rock, *Gillis* 3776 (MSC). STONE CO.: Ozark National Forest, rocky creek above Blanchard Springs, Allison, *Demaree* 52504 (MSC). **Louisiana.** New Orleans, *Cocks* 67 (A); 3 miles north of Maurepas, *Seibert* 703 (MO); Hammond, 13 miles east of city, *Rose-Innes & Warnock* 721 (GH, TEX). **Mississippi.** DESOTO CO.: 3 miles north of Nesbitt, *Gillis* 5906 (MSC). JACKSON CO.: Ocean Springs, *Demaree* 28099 (SMU). **Oklahoma.** LEFLORE CO.: Stapp, creek banks, *Demaree* 15732 (MO, NY, SMU).

Toxicodendron radicans subsp. **negundo** × subsp. **radicans.** Table 8.

Rhus radicans forma *hypomalaca* Fernald, Rhodora 43: 592. 1941. Type: West Virginia, Ritchie Co., Berea, dry upland woods. *L. F.* and *F. R. Randolph* 1385, 23 August 1922. (GH, holotype).

Representative specimens: UNITED STATES. **Arkansas.** DREW CO.: Monticello, *Demaree* 13692 (A, NY). GARLAND CO.: Starlight Bay, Hot Springs National Park, *Demaree* 54056 (MSC). JOHNSON CO.: Knoxville, *Demaree* 19943 (MIN). PERRY CO.: Ouachita National Forest, *Demaree* 37842 (SMU). PULASKI CO.: Galloway near Little Rock, *Demaree* 53848 (MSC). **District of Columbia:** Washington, Hunting Creek, *Ward*, s.n. (US); Giesboro Road, *Steele*, s.n. (US). **Kentucky.** BREATHITT CO.: Robinson Forest, *Smith* 1717 (KY). OLDHAM CO.: 3 miles SE of Westport, *Duncan* 22750 (KY). **Louisiana.** MADISON PARISH: Tensas Gun Club Refuge, *Ewan* 17578 (MO). ORLEANS

PARISH: New Orleans, *collector unknown* (E). PLAQUEMINES PARISH: Pillottown, *Ewan* 17486 (MO). ST. MARY PARISH: Cote Blanche Island, *Thieret* 17443 (MSC). **Massachusetts.** BERKSHIRE CO.: without definite locality. *Milligan*, s.n. (ARIZ). BRISTOL CO.: Nunquit, part of Dartmouth, *Sturtevant*, s.n. (MIN). ESSEX CO.: Bradford, part of Haverhill, *Churchill*, s.n. (MIN). NORFOLK CO.: West Quincy, *Churchill*, s.n. (MIN). **Mississippi.** DESOTO CO.: 3 miles north of Nesbit, *Gillis* 5906 (MSC). **North Carolina.** BUNCOMBE CO.: Asheville, *Donahue* 259, (MSC). SWAIN CO.: Alarka, *Ahles & Bell* 14210 (FLAS). **Pennsylvania.** BEDFORD CO.: without definite locality, *Westerfield* 6568 (SMU). CHESTER CO.: Berwyn, Darby Creek, *Stone*, s.n. (RM). HUNTINGDON CO.: Raystown Branch, 1 mile NE of Entriken Bridge, *Wahl, Handwerk, & Westlake* 5627 (FLAS). JUNIATA CO.: Port Royal, *Fogg* 16858 (NY). ADAMS CO.: South Piney Mt., *Gillis* 5112 (MSC). FRANKLIN CO.: east slope of Tuscarora Mt., *Gillis* 5110 (MSC); near summit, east slope of Tuscarora Mt., *Gillis* 5114 (MSC). **Tennessee.** FRANKLIN CO.: without definite locality, *Eggert*, s.n. (MO). **Texas.** BEXAR CO.: Rio Medina, *Berlandier* 2475, 1045 (E, GH); SMITH CO.: Tyler, *Moore* 580 (GH). **Virginia.** BEDFORD CO.: without definite locality, *Curtiss*, s.n. (GH). FREDERICK CO.: Winchester, *Gillis* 5702 (MSC). FLOYD CO.: State highway near Blue Ridge Parkway, *Donahue* 260 (MSC). JAMES CITY CO.: Toano, *Menzel*, s.n. (GH). MONTGOMERY CO.: East Bradford, *Adams & Wherry* 2263 (GH). SMYTH CO.: Marion, *Britton & Wail*, s.n. (F, NY). **West Virginia.** GREENBRIER CO.: Blue Bend Recreation Area, *Donahue* 263 (MSC). MORGAN CO.: near B. & O. Railroad and Potomac River, *Donahue* 266 (MSC). TAYLOR CO.: Thornton, *Gillis* 5723 (MSC).

Whereas *Toxicodendron radicans* subsp. *radicans* is primarily an Atlantic Seaboard taxon and subsp. *negundo* is a land-locked taxon of the Midwest and the Ohio River Valley, their ranges come into contact in the Piedmont, the lower Appalachians and west in Arkansas. Characters separating these taxa are more subtle than those separating many others; it is therefore not always easy to determine with assurance what may be an extreme form of one of the parents, or what may actually be a hybrid. It is on the basis of certain key characters, however, that determinations of suspected hybrid origin have been made. These characters are listed in Table 8.

Although Fernald intended to differentiate forma *hypomaloca* from others by the pilose lower leaf surfaces, the type specimen actually represents an intermediate between Coastal poison-ivy (subsp. *radicans*) and the midwestern taxon (subsp. *negundo*). The pilosity of the lower leaf sur-

TABLE 8. CHARACTERS OF PARENTS TOXICODENDRON RADICANS SUBSP. NEGUNDO AND SUBSP. RADICANS

Toxicodendron radicans subsp. *radicans*	Putative Hybrid	*T. radicans* subsp. *negundo*
Petioles sparsely pubescent	Petioles puberulent to sparsely strigose	Petioles strigose
Leaflets entire	Leaflet margin with prominent notches, or undulate or serrate	Leaflets notched or serrate
Lower leaflet surface with tufts of hairs in vein axils	Lower leaflet surface with a few hairs concentrated in vein axils	Lower leaflet surface without tufts of hairs in vein axils
Fruits pubescent	Fruits with scattered hairs or incipiently papillose	Fruits glabrous

faces is interpreted as a local variation. It is perhaps the result of the proper "dose" of additive genes. The fruits have a few scattered hairs and papillae, suggestive of *Toxicodendron radicans* subsp. *radicans*, but the leaflets are notched and acuminate in the fashion of subsp. *negundo.* Since the specimen comes from the mountains of West Virginia which form part of the barrier between these two taxa, it is not unlikely that intermediate forms should be found. (Fig. 54.)

HYBRIDS WITH T. RYDBERGII

Toxicodendron diversilobum × rydbergii. Table 9.

Toxicodendron lobadioides Greene, Leaf. Bot. Observ. Crit. 1: 119. 1905. Type: Washington, Western Klickitat County along the Columbia River, rocky places. *W. N. Suksdorf*, s.n., July 1885. (US-47202, holotype; F-155984, F-255875, isotypes in part).

Toxicodendron coriaceum Greene, Leafl. Bot. Observ. Crit. 1: 120. 1905. Type: Washington Territory, *W. N. Suksdorf*, s.n., 6 May 1885. (US-19803, holotype; DS-85511, F-155984 (in part), F-255875 (in part), MO-1773719, NY, isotypes).

Representative specimens: UNITED STATES. **Oregon.** HOOD RIVER CO.: Hood River, near mouth of river on floodplain, *Gillis* 5237 (MSC); same, *Whited* 1117 (ND); same, rocky bluffs, *Henderson* 305 (MO). WASCO CO.: The Dalles, *Howell*, s.n. (GH), *Gillis* 4222 (MSC); Seufert, *Gillis* 4232 (MSC). SHERMAN CO.: east of Rufus, *Gillis* 4230 (MSC). **Washington.** KLICKITAT CO.: western part of county, *Suksdorf*, s.n. (DS, F, GH, MO, NY, US); roadside park near confluence of Klickitat and Columbia Rivers, *Gillis* 5240 (MSC); 11.2 miles east of Klickitat River confluence with Columbia, *Gillis* 5241 (MSC); 11.3 miles east of confluence of Klickitat and Columbia Rivers, *Gillis* 5242 (MSC); Murdock, east of bridge, *Gillis* 5343 (MSC); savanna valley, T. 2N., R. 15E., SW 1/4 Sec. 11, *Gillis* 5244 (MSC).

Presumably the two Greenean species are hybrids between *Toxicodendron rydbergii* and *T. diversilobum* for they were collected in the region where the two species overlap in range. They are probably part of the same population, from the basaltic washes in the hills near the confluence of the Columbia and Klickitat Rivers in western Klickitat County, Washington.

TABLE 9. CHARACTERS OF PARENTS, TOXICODENDRON DIVERSILOBUM AND T. RYDBERGII, AND THEIR PUTATIVE HYBRID OFFSPRING

T. diversilobum	Putative Hybrid	*T. rydbergii*
Petiole glabrate or puberulent	Petiole glabrate	Petiole glabrous
Leaves 7-10 per 10 cm twig	Leaves 4-10 per 10 cm twig	Leaves 4-5 per 10 cm twig
Leaflets serrate, undulate, or lobed	Leaflets entire, or with undulating margin	Leaflet margins undulate
Leaflets broadly elliptic, obovate, or suborbicular	Leaflets broadly ovate	Leaflets broadly ovate to suborbicular
Leaflets glabrous below, or with few scattered hairs	Leaflet glabrate to strigose below	Leaflets glabrous or appressed strigose below
Leaflet tips obtuse	Leaflet tips acute to slightly acuminate	Leaflet tips acute or acuminate
Fruits 6-7 mm broad	Fruits 5-6.5 mm broad	Fruits 4.5-5.5 mm broad
Fruits flattened, obliquely deltoid	Fruits slightly flattened, subglobose	Fruits globose
Fruits glabrous	Fruits setulose or papillose	Fruits globose

Data on an isotype of *Toxicodendron coriaceum* and of *T. lobadioides* at F suggests that one population which was sampled by Suksdorf on two different occasions furnished the type material for two of Greene's species! This sheet has both a fruiting and a flowering specimen and bears a printed label indicating the date of collection as "May 6, July 1885." The holotype of *T. coriaceum* at US is a match for the fruiting representative except that it bears a handwritten label. The type of *T. lobadioides* at US is a match for the flowering representative on the sheet at F, but bears copies of both the handwritten and printed labels. Also, the isotypes of *T. coriaceum* at NY and at MO have the printed label with the May date crossed out.

Presumably the flowering specimen dates from May, and the fruiting one from July, both from the same general area, representative of the same or closely related populations. The two type specimens mentioned above appear to be intermediate in morphology between *Toxicodendron diversilobum* and *T. rydbergii.* Whereas *T. diversilobum* has densely short-pubescent fruits and *T. rydbergii* has glabrous fruits, these intermediates have scattered hairs, or in one instance, a crown of hairs at the base of the fruit. Table 9 shows the diagnostic characters used in analyzing these intergrades.

Because of the already burdensome collection of names that the poison-ivy complex has acquired, I have preferred to use a formula to designate this hybrid, rather than use either of the Greene names, or some other at the subspecies level. Moreover, no one population possesses the same cluster of intermediate characters nor the whole array of them, so that a hybrid taxon would be difficult to circumscribe. The formula seems to be a better means to indicate a specimen or population that demonstrates intermediate characters anywhere along the spectrum between one parental form and the other.

Toxicodendron radicans subsp. **divaricatum** × **T. rydbergii.** Table 10.

These two taxa are relatively uncommon throughout their

TABLE 10. CHARACTERS OF PARENTS, TOXICODENDRON RADICANS SUBSP. DIVARICATUM AND T. RYDBERGII, AND THEIR PUTATIVE HYBRID OFFSPRING

T. radicans subsp. *divaricatum*	Putative hybrid	*T. rydbergii*
Aerial roots present; plant often climbing	Aerial roots present; plant climbing to 3 meters	Aerial roots absent; plant never climbing
Petiole thinly to thickly puberulent	Petiole glabrous or puberulent	Petiole always glabrous
Petiole shorter than terminal leaflet	Petiole about the same length or longer than terminal leaflet	Petiole usually very long; usually much longer than terminal leaflet
Leaflets 1.9-3 times as long as broad	Leaflet 1.3-1.6 times as long as broad	Leaflets broadly ovate to suborbicular, 1.1-1.5 times as long as broad
Leaflet margins entire	Leaflet margins dentate	Leaflet margins dentate or undulate
Fruits glabrate in northern part of range (Arizona)	Fruits with scattered pubescence	Fruits always glabrous

respective ranges, but especially so in the arid and semi-arid regions of southern Arizona and northern Sonora. Suspected intermediates have been found in only three places: in the Chiricahua Mountains and the Santa Rita Mountains of Arizona and the San José Mountains of Sonora. The characteristics which appear to intergrade are listed in Table 10.

Representative specimens: MEXICO. **Sonora:** San José Mountains, *Mearns* 1052 (US). UNITED STATES. **Arizona:** SANTA CRUZ CO.: Florida Canyon, Santa Rita Mountains, 4000 feet, *Graham*, s.n. (NY). COCHISE CO., above Portal, Chiricahua Mountains, 5000 feet elevation. *Stoutamire* 3986 (BLH, MSC).

Toxicodendron radicans subsp. **negundo** × **T. rydbergii.** Table 11.

Toxicodendron rufescens Greene, Leafl. Bot. Observ. Crit. 2: 46. 1910. Type: Indiana, Marshall County, vicinity of Lake Maxinkuckee, *H. Walton Clark* 2, 14 September 1906 (US-645163, holotype).

Representative specimens: UNITED STATES. **Illinois.** WILL CO.: Romeoville (formerly Romeo), *Umbach*, s.n. (F, WIS). Locality uncertain: *Gates* 745 (F). **Indiana.** MARSHALL CO.: Lake Maxinkuckee, *Clark* 2 (ND-G, US). **Michigan.** GLADWIN CO.: Sage Twp., shore of Wiggins Lake, *Gillis* 3602 (MSC). LAPEER CO.: Imlay City, *Farwell* 6693 (BLH). OSCODA CO.: south of Oscoda, *Hagenah* 2365 (BLH). ST. CLAIR CO.: Port Huron, *Dodge*, s.n. (MIN). **Minnesota:** Spring Grove, *Rosendahl* 280 (GH). **New York.** CHEMUNG CO.: without definite locality, *Lucy* 1694 (F, RM, WIS). LEWIS CO.: Harrisville, *Gillis* 5377 (MSC). **Oklahoma.** BEAVER CO.: Knowles, *Stevens* 516 (GH, MIN, MO, NY). **South Dakota.** UNION CO.: Ravine, T. 92N., R. 49W., *Eslick*, s.n. (SDU). **West Virginia.** KANAWHA CO.: Quick, *Reed*, s.n. (CHRB). **Wisconsin.** SAUK CO.: *Smith* 7984 (A, MIL, WIS).

CANADA **Ontario.** WATERLOO CO.: Hamburg, river banks. *Merner* 15031 (WIS); **Québec.** LAVAL CO.: St.-Laurent, *Adrien* 1088 (A, GH).

Greene (1900) thought his species *Toxicodendron rufescens* to be near *T. glabrum* Mill. or *Rhus littoralis* Mearns (= *T. radicans* subsp. *radicans*). It appears rather to be an intermediate between *T. radicans* subsp. *negundo* and *T. rydbergii*, with fruits and petiole length in common with the former and leaflet shape, habit, and absence of aerial rooting of the latter. Both taxa are known from this general region of Indiana.

The two parental taxa are very different from one another when they show the most definitive characters, but not all specimens seen in the field, or worse yet, in the herbarium, demonstrate the most important diagnostic characters. A fruiting specimen with tight, erect inflorescences, fruits greater than 0.5 cm broad, very long, glabrous petioles, and suborbicular leaflets is unquestionably *Toxicodendron rydbergii*. A flowering male specimen with puberulent petioles and broadly ovate leaflets is not so easily pigeonholed. It has been mentioned earlier that subsp. *negundo* is difficult to characterize because it has much in common with several other taxa and is characterized more because of what striking characters it does *not* possess, than because of those it does. Along the zone of overlap in the ranges of *T. rydbergii* and *T. radicans* subsp. *negundo*, the characters which distinguish these taxa become blurred. A number of populations in this tension zone look suspiciously like intergrades between the two parental forms.

The regions where the two ranges meet are: the southern lobe of Ontario, the central part of the Lower Peninsula of Michigan, areas around the southern half of Lake Michigan, and an irregular line cutting southwest across Illinois, Iowa, Nebraska, and Kansas, and through parts of Oklahoma. Suspected intermediates have been examined in the herbarium and a few in the field from this region. (Fig. 54.) The suspected hybrids show their intermediate nature as indicated in Table 11.

Toxicodendron radicans subsp. **radicans** × **rydbergii.** Table 12.

Toxicodendron rydbergii and *T. radicans* subsp. *radicans* have ranges which meet in the northern United States and bordering Canada east of the Appalachian Mountains and the Laurentian Plateau. Where their ranges overlap, there appears to be some introgression. A number of specimens have been seen from Quebec, Nova Scotia, the Berkshire Mountains, and other places in southern New England which appear to be intergrades between these two taxa. (Fig. 54.) The characters upon which their hybrid nature has been suspected are listed in Table 12.

TABLE 11. CHARACTERS OF PARENTS, T. RADICANS SUBSP. NEGUNDO AND RYDBERGII, AND THEIR PUTATIVE HYBRID OFFSPRING

T. radicans subsp. *negundo*	Putative Hybrid	*T. rydbergii*
Shrub or vine with aerial roots	Sub-shrub or climbing vine; aerial roots may or may not be present	Sub-shrub
Petioles puberulent or strigose	Petioles glabrous, puberulent, or scattered hairy	Petioles glabrous
Petioles averaging less than 10 cm long	Petioles averaging about 15 cm long	Petioles 8-18 cm long
Leaflets ovate	Leaflets broadly ovate	Leaflets suborbicular
Leaflets coarsely toothed	1-2 teeth on leaflets	Leaflets with 1-8 pairs of notches or serrations
Fruits averaging less than 0.45 cm in diameter	Fruits ranging between 0.4 and 0.5 cm in diameter	Fruits averaging 0.5 cm in diameter

TABLE 12. CHARACTERS OF PARENTS, TOXICODENDRON RADICANS SUBSP. RADICANS, AND T. RYDBERGII AND THEIR PUTATIVE HYBRID OFFSPRING

Toxicodendron rydbergii	Putative Hybrid	*T. radicans* subsp. *radicans*
Sub-shrub	Sub-shrub; few plants climbing by aerial roots	Shrub or climbing vine
Petioles averaging more than 15 cm	Petioles averaging 12 cm	Petioles averaging less than 10 cm
Petioles glabrous	Petioles glabrous or becoming puberulent distally	Petioles glabrate or puberulent
Leaflets broadly ovate to suborbicular	Leaflets broadly ovate	Leaflets ovate or elliptic
Lower leaflet surface with no concentration of hairs in vein axils	Lower leaflet surface with few hairs in vein axils	Lower leaflet surface with concentration of hairs in vein axils
Upper leaflet surface glabrous	Upper leaflet surface glabrous	Upper leaflet surface glabrate
Leaflet margins serrate or undulate	Leaflet margins undulate or entire	Leaflet margins entire
Fruits averaging 0.5 cm in diameter	Fruits variable in size, but averaging 0.45 cm in diameter	Fruits averaging 0.4 cm in diameter
Exocarp glabrous	Exocarp incipiently papillose; some with scattered hairs, or glabrous	Exocarps pubescent or papillose

Representative specimens: UNITED STATES. **Connecticut.** LITCHFIELD CO.: 2.5 miles SE of Washington, *Donahue* 267 (MSC); near Massachusetts line, *Fernald*, s.n. (GH). **Maine.** KNOX CO.: Rockland, *Fernald* 1994 (GH). **Massachusetts.** BERKSHIRE CO.: Hoosac Valley, Lanesboro, *Churchill* 552 (IN). ESSEX CO.: Bradford, part of Haverhill, *Churchill*, s.n. (MO). SUFFOLK CO.: Dorchester, section of Boston, *Churchill* 552 (MO). **New Hampshire.** STRAFFORD CO.: NE of Durham, *Donahue* 268 (MSC). GRAFTON CO.: West Thornton, *Gillis* 4097 (MSC). MERRIMACK CO.: Concord, *Gillis* 4100 (MSC). **Pennsylvania.** MIFFLIN CO.: without definite locality, *Rothrock*, s.n. (F). **Rhode Island.** PROVIDENCE CO.: Diamond Hill, *Palmer* 46188 (A). **Tennessee.** BLOUNT CO.: Walland, *Hudson*, s.n. (RM). **Vermont.** CALEDONIA CO.: Barnet, *Blanchard*, s.n. (MIN, MO, NY, US). LAMOILLE CO.: without definite locality, *Grout*, s.n. (F). WINDSOR CO.: Ascutney, *Gillis* 4088 (MSC). **Virginia:** 1 mile north of Hopewell Gap, western slope of Bull Run Mts., *Allard* 462 (GH, US). **West Virginia.** HAMPSHIRE CO.: Slanesville, *Donahue* 265 (MSC).

CANADA. **Nova Scotia.** HALIFAX CO.: Fall River, *Jack* 3317 (MO). LUNENBERG CO.: East Bridgewater, *Macoun* 81289 (F). **Québec.** BROME CO.: Glen Sutton along the Missiquoi River, *Marie-Victorin, et al.* 56209 (GH, F, MO, NY).

HYBRIDS WITH T. TOXICARIUM

Toxicodendron radicans subsp. **radicans** × **toxicarium.** Table 13.

Suspected hybrids between these two species have been found along the American Atlantic Seaboard where their ranges overlap. Because their habitat requirements are generally quite different, it is not often that a pollinating vector will visit one parent plant while carrying pollen from the other. Criteria which were employed for determination of these forms as hybrids are given in Table 13.

Representative specimens: UNITED STATES. **Alabama.** COVINGTON CO.: edge of titigum — magnolia bay, 17 miles SSW of Andalusia, *Hardin & Duncan* 15010 (GA). **Arkansas.** CONWAY CO.: Morrilton, *Demaree* 23089 (GH, MIN, MO, NY, SMU). LOGAN CO.: Blue Mountain, *Palmer* 24810 (MO). **Georgia.** BIBB CO.: savanna woodland, *Gillis* 6575 (MSC). WALKER CO.: rocky area below Harrisburg, 10.3 miles SW of Lafayette, *Hardin, Humphrey & Duncan* 13872 (GA). **North Carolina.** FORSYTH CO.: Kernersville, *Ahles & Britt* 40711 (NY). STANLEY CO.: Yadkin River, southeast of Badin, *Ahles & Radford* 11936 (SMU). **South Carolina.** PICKENS CO.: Clemson College (MO). RICHLAND CO.: north of Columbia on highway 21, pine woods, *Gillis* 4582 (MSC). **Virginia.** FAUQUIER CO.: Bull Run Mts., *Allard* 9941 (GH).

TABLE 13. CHARACTERS OF PARENTS, TOXICODENDRON RADICANS SUBSP. RADICANS AND T. TOXICARIUM, AND PUTATIVE HYBRID OFFSPRING

Toxicodendron toxicarium	Putative Hybrid	*T. radicans* subsp. *radicans*
Sub-shrub	Shrub or vine	Shrub or vine
Petioles hirsute or tomentose	Petioles hirsute or strigose	Petioles sparsely pubescent
Leaflet with lobed or undulating margins	Leaflet with sharp lobes, or with coarsely serrate or crenate margins	Leaflet with entire margins, or rarely notched
Leaflets ovate to oblong or oblong-obovate	Leaflets rhomboid to broadly ovate or elliptic	Leaflets ovate or elliptic
Upper leaflet surface scabrous or hispid	Upper leaflet surface sparingly pubescent	Upper leaflet surface glabrate
Lower leaflet surface hirsute or velutinous	Lower leaflet surface velutinous	Lower leaflet surface glabrous or glabrate
Fruit pubescent and often papillose	Fruits rare	Fruits pubescent
Leaflet margins ciliate	Leaflet margins ciliate	Leaflet margins not ciliate
Lower leaflet pubescence uniformly distributed or perhaps heaviest along midrib	Lower leaflet with tufts of hairs in vein axils	Lower leaflet with tufts of hairs in vein axils

Toxicodendron radicans subsp. **verrucosum** × **toxicarium.** Table 14.

This hybrid is likely to be a limited one because the two parental types are sympatric for only a small portion of their total range. Moreover, *Toxicodendron toxicarium* tends to be found in rather acidic soils and *T. radicans* subsp. *verrucosum* is generally found in more alkaline soils or in shallow lithosols derived from limestone. Several populations in Texas, however, have produced suspected hybrids, plants which are intermediate in morphology between the two taxa. (See Table 14.)

Representative specimens: UNITED STATES. **Texas.** ARANSAS CO.: *Cory* 49016 (GH). BASTROP CO.: climbing post oak in Bastrop State Park, *Gillis* 5167 (MSC). BEXAR CO.: San Antonio, *Jermy* 326 (GH); MCLENNON CO.: Robinson, *Cory* 55710 (SMU). RED RIVER CO.: Clarkville along Red River, *Cory* 5604 (SMU). White Oak Bayou, collector and county unknown (MIN).

UNCERTAIN OR EXCLUDED SPECIES

Rhus-Toxicodendron radicans Marshall, Arbust. Am. p. 131. 1785. This name probably refers to *Toxicodendron radicans*, but there is neither citation of previous published names nor of any specimens.

Rhus-Toxicodendron toxicodendrum Marshall, Arbust. Am. p. 131. 1785. This name probably refers to *Toxicodendron toxicarium*, but there is neither citation of previous published names nor of any specimens.

Toxicodendron vulgare Mill. Gard. Dict. ed 8, Art. *Toxicodendron*, No. 1. 1768. The description can apply to a number of taxa. No specimen to represent this name can be found.

Toxicodendron pubescens Mill. Gard. Dict. ed. 8, Art. *Toxicodendron*, No. 2. 1768. The description can apply to a number of taxa. No specimen to represent this name can be found.

Toxicodendron crenatum Mill. Gard. Dict. ed. 8, Art. *Toxicodendron*, No. 5. 1768. The description can apply to a number of taxa. No specimen to represent this name can be found.

TABLE 14. CHARACTERS OF TOXICODENDRON RADICANS SUBSP. VERRUCOSUM AND T. TOXICARIUM AND THEIR PUTATIVE HYBRID OFFSPRING

Toxicodendron toxicarium	Putative Hybrid	*T. radicans* subsp. *verrucosum*
Sub-shrub	Small shrub or vine	Shrub or vine
Aerial roots absent	Aerial roots present	Aerial roots present
Leaflet lobes rounded	Leaflet lobes obtuse	Leaflet lobes angular
Lower leaflet surfaces pilose to velutinous	Lower leaflet surfaces pilose	Lower leaflet surfaces glabrous or glabrate
Fruits pubescent or papillose	Fruits with scattered pubescence and papillae	Fruits glabrous

Toxicodendron volubile (as "*volubilis*") Mill. Gard. Dict. ed. 8, Art. *Toxicodendron,* No. 6. 1768. *Rhus radicans* var. *volubile* (Mill.) DC. Prodr. p. 69. 1825. *Rhus toxicodendron* subsp. *vulgaris* var. *volubilis* Engler in DC. Monog. Phaner. 4: 394. 1883. *T. radicans* var. *volubile* Farwell, Amer. Midl. Naturalist 12: 125. 1930. All uses of the epithet *volubilis* refer to Miller or DC, the former of whom equates his species to *Toxicodendron amplexicaule* . . . of Dillenius. None of these plants can be typified. They probably refer to some kind of *T. radicans,* but which subspecies is uncertain. Engler cites "*Rh. Toxicodendron* L. Spec. 381 sensu stricto" but describes it as "caule scandente, vix radicante" which does not accurately describe *Rhus Toxicodendron* sensu stricto. He further cites a large number of specimens, some at Kew and some presumably then at Berlin, but these specimens represent almost every taxon in the poison-ivy complex.

Toxicodendron serratum Mill. Gard. Dict. ed. 8, Art. *Toxivodendron,* No. 7. 1768. No specimen to represent this name can be found.

Toxicodendron arborescens Mill. Gard. Dict. ed. 8, Art. *Toxicodendron,* No. 9. 1768. The description can fit most taxa in the poison-ivy complex. No specimen to represent this name can be found.

Rhus pumilum Pursh, Fl. No. Am. 1: 205. 1814. (= *R. michauxii* Sarg.).

Rhus variifolium DC. Prodr. 2: 73. 1825. Nomen nudum.

Rhus bahamensis D. Don. 1832. A General System of Gardening and Botany, p. 72. London. 1832. Nomen nudum. This is possibly *Toxicodendron radicans* subsp. *radicans,* the only member of the *Rhus* complex known from the Bahamas.

Rhus quercifolia Goeppert, Tert. Fl. Schossnitz. 1855 (= *Monopleura* in Aceraceae).

(To be concluded)

STRUCTURE AND VARIATION IN SPORES OF THELYPTERIS PALUSTRIS

ALICE F. TRYON

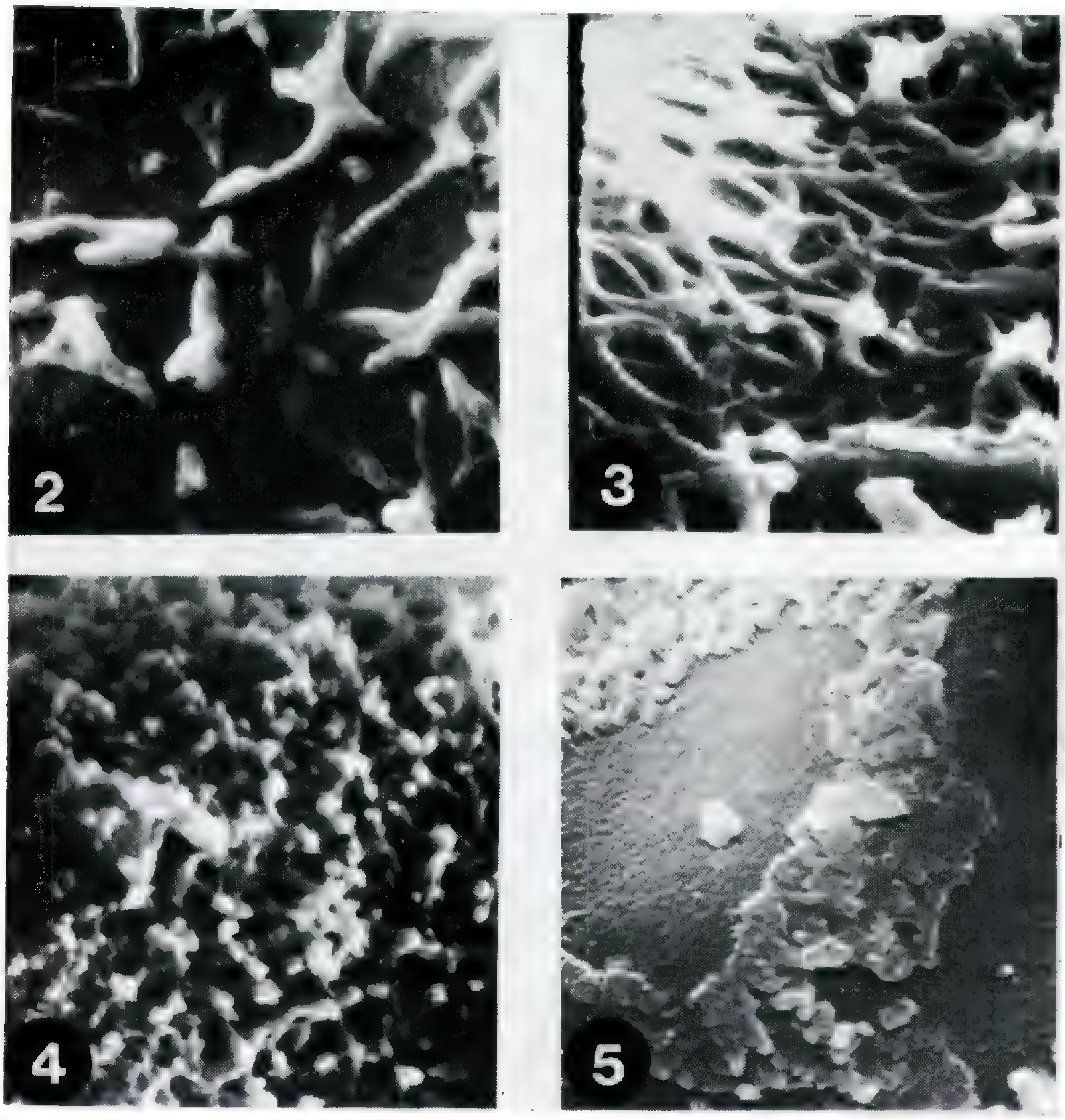
The Marsh Fern is abundant in New England growing in wet, usually open places, often bordering Red Maple woods. It frequents wet sites such as open bogs or swampy stream banks, over a wide geographic range — across Eurasia, in India and Burma, in Africa from the Cameroons and Kenya to Cape Province in the Republic of South Africa, in New Zealand, New Guinea and Sumatra, as well as North America (Fig. 1). Spores from plants of different geographical regions, examined with the scanning electron microscope, show exceptional differences in perine sculpture. The usual variation in the perine layer of spores of *Thelypteris palustris* is assessed in relation to spore development and to the geographical varieties. In other species of ferns and often within genera the spores are relatively similar in sculpture. Indeed, the uniformity by which these patterns are usually replicated demonstrates remarkably regulated morphogenetic systems.

The four varieties of *Thelypteris palustris* Schott, designated by Fernald (1929), included var. *pubescens* (Lawson) Fernald of northeastern North America and eastern Asia; var. *Haleana* Fernald of the southeastern United States and Bermuda; var. *palustris* (Fernald's var. *typica*) of Eurasia; and var. *squamigera* (Schlecht.) Weatherby of Africa, India, Burma, New Zealand and more recently reported from Sumatra and New Guinea. Treatment of these as a single species, as noted by Morton (1967), now requires the application of an earlier name, *Thelypteris confluens* (Thunb.) Morton, based upon a South African collection. In a comparative survey of *Thelypteris* with three other genera, Holttum, Sen and Mittra (1970) note that var. *squamigera* might be better treated as a separate species, and that the status of Fernald's other varieties needs further consideration. The well-known name *Thelypteris palustris* is used here, pending definitive systematic studies of greater scope and further clarification of names.

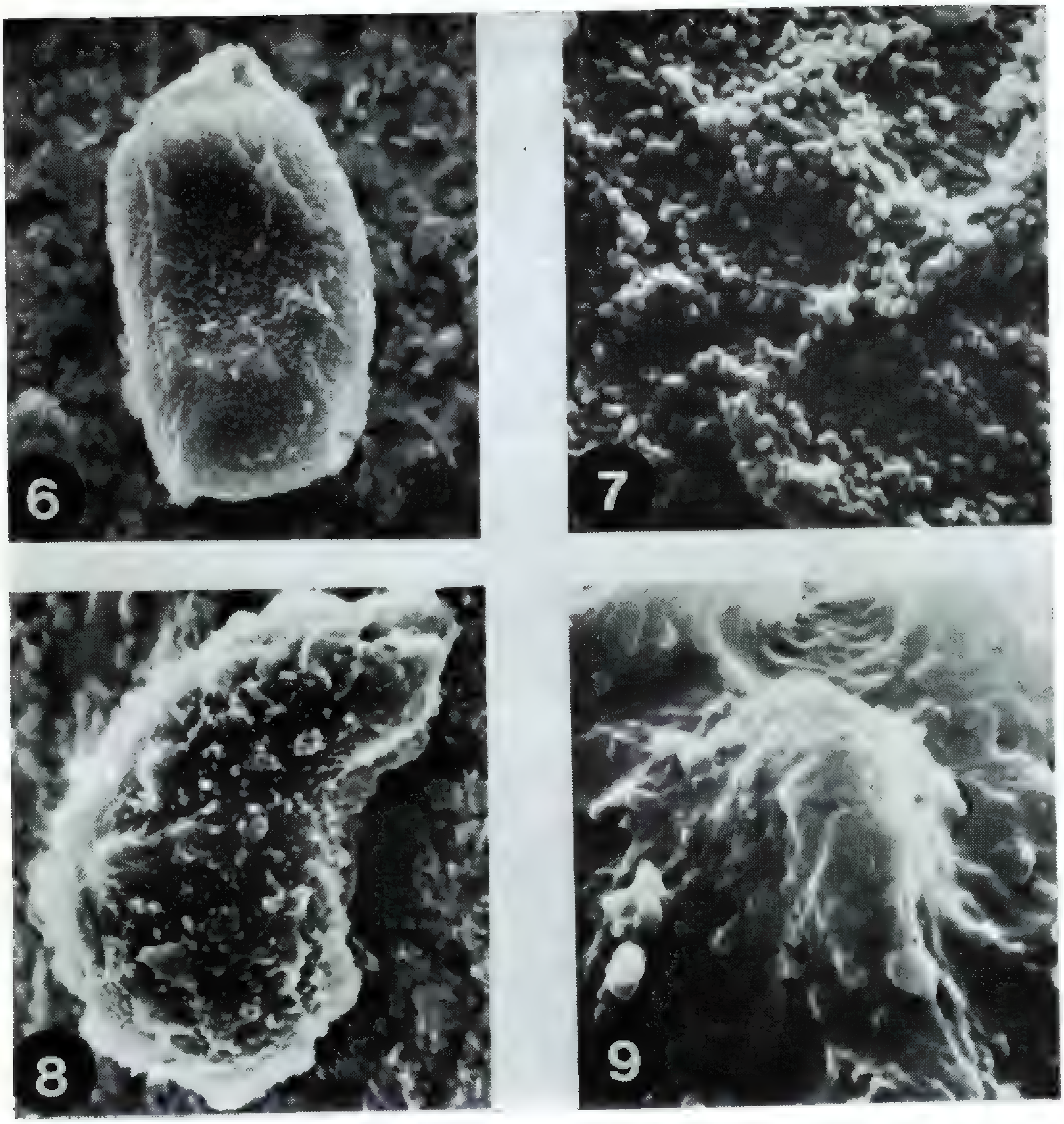
MATERIALS AND METHODS

The collections of *Thelypteris palustris* in the Gray Herbarium have been the principal source for this study; some materials from the United States National Herbarium (Smithsonian Institution) have also been used. Citations of collections are included where they are appropriate and in captions for figures. Plants of var. *pubescens* from Maine, New York, Wisconsin, and population samples from several localities in eastern Massachusetts have been used for study of stages in spore wall development. These specimens were grown at the same site, along with native plants, in Lexington, Massachusetts. The native Lexington material has been most extensively studied and a voucher for this (*A. F. Tryon* 70-18) as well as the other transplanted specimens, are deposited in the Gray Herbarium.

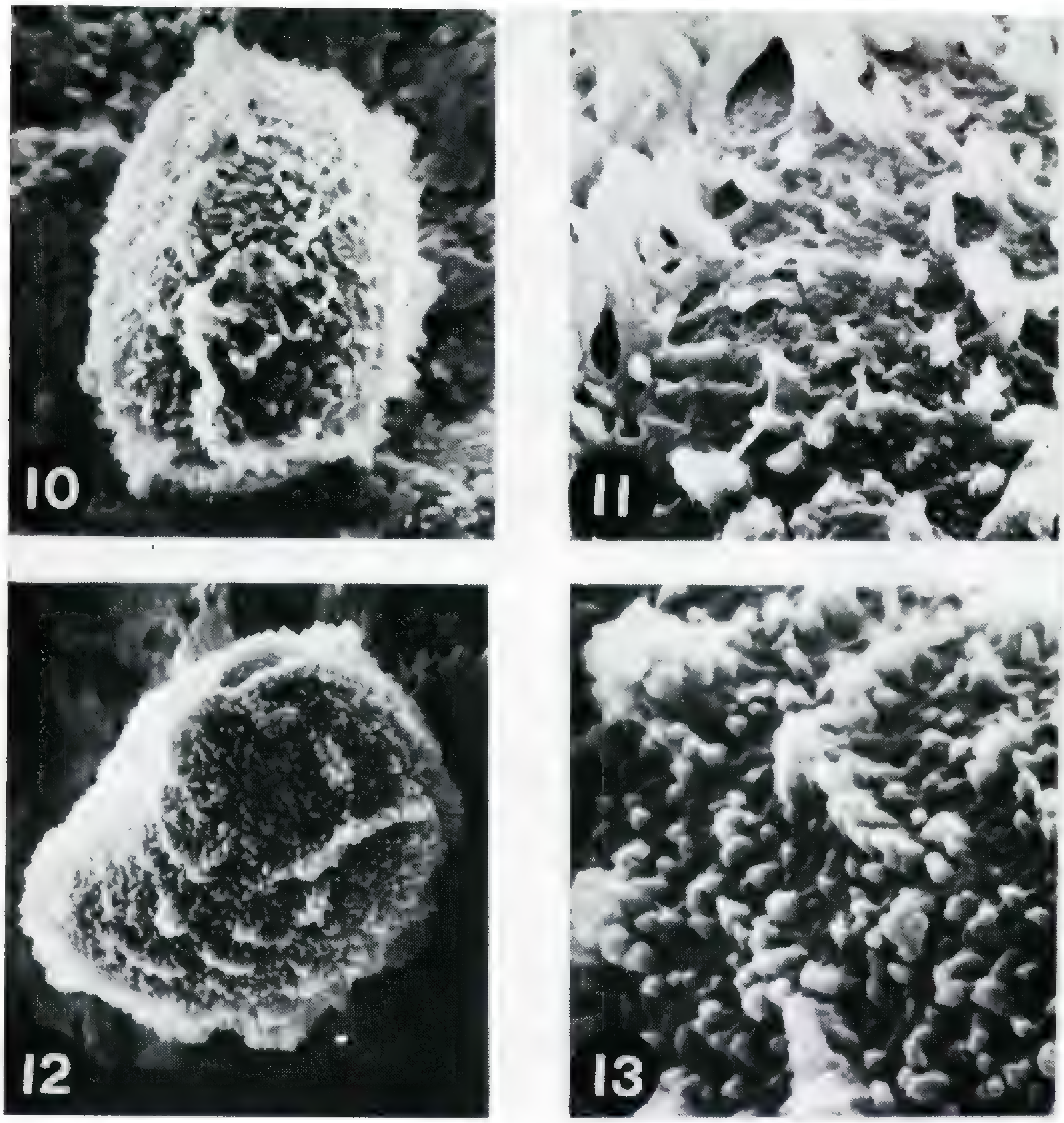
The descriptions of spores of each variety are drawn from specimens studied with both light and scanning electron microscopes. Preparation for the latter were made from non-acetolized spores from herbarium specimens and were prepared by two methods. Those done at the University of Illinois, Chicago Circle, in the laboratory of Dr. Thomas N. Taylor are illustrated in Figs. 6, 8, 9, 10-13, 16, 17, 19, 20. They were gathered in distilled water, dried and fixed on standard aluminum specimen stubs with a thin layer of silver conductive paint. They were coated with evaporated gold while rotating the sample to insure even deposition. Other spores, illustrated in Figs. 2-5, 7, 14, 15, 18, 21, 22, were gathered with a dry brush and transferred onto double-stick Scotch tape fixed to the aluminum stubs. These specimens were undercoated with carbon prior to coating with an evaporated alloy of palladium-gold while on a rotating and tilting platten. The original magnifications of the photographs of whole spores were between 1,000 and 2,000 times; the details were photographed between 5,000 and 10,000. The plates are reduced approximately one-third. Spore size is regarded as approximate because of differences in magnification factors on the different instruments. Some artifacts are conspicuous at the



Figs. 2-5. Surface of spores of *Thelypteris palustris* var. *pubescens*, *Pammel* 579, Iowa (GH); Figs. 2, 3. Partial deposition of perine layer, × 6600; Fig. 4. Complete deposition of perine layer, × 3300; Fig. 5. Partially eroded perine material exposing smoother exine layer, × 3300.

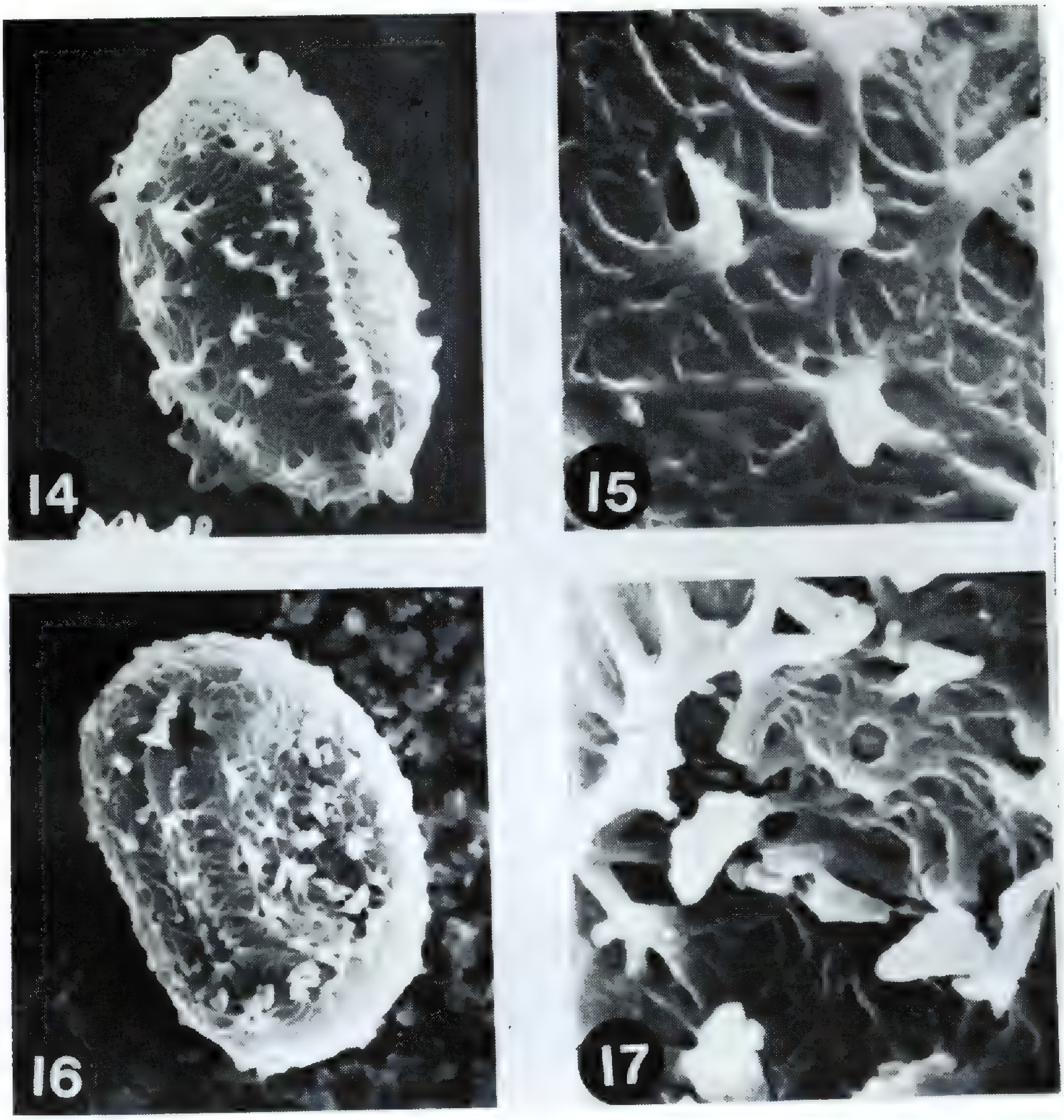


Figs. 6-9. Spores of *Thelypteris palustris* var. *pubescens:* Figs. 6, 7. *A. F. Tryon* 70-18, Lexington, Massachusetts (GH); Fig. 6. Spore with verrucate perine layer (the exine layer is exposed in the break, at the top of the spore) × 860; Fig. 7. Papillate surface of the perine layer, × 4400; Figs. 8, 9. *Clements* 293b, Nebraska (GH); Fig. 8. Spore with irregularly sculptured perine layer, × 1000; Fig. 9. Papillate and coarser projections, × 3500.

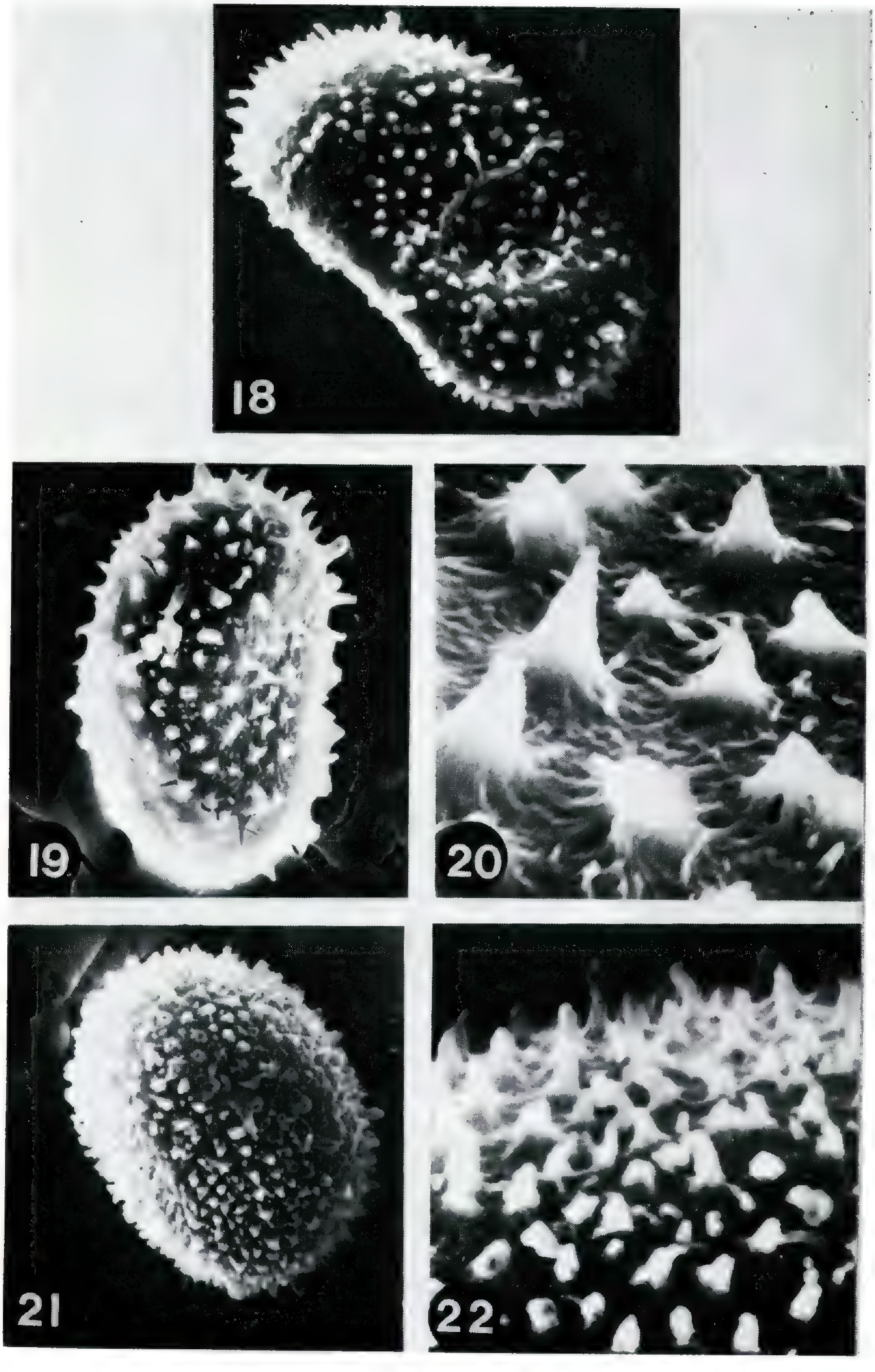


Figs. 10, 11. Spore of *Thelypteris palustris* var. *pubescens*, *Furse*, in 1957, Hondo, Japan (GH); Fig. 10. Spore with basal reticulum, papillae and higher ridges, × 650; Fig. 11. Papillae, areolae and basal reticulum, × 3500.

Figs. 12, 13. Spore of *Thelypteris palustris* var. *Haleana*, *Bloomquist & Correll* 6136, Florida (GH); Fig. 12. Spore with papillate perine layer and more prominent ridges, × 1000; Fig. 13. Papillae and short ridges, × 3600.



Figs. 14-17. Spores of *Thelypteris palustris* var. *palustris:* Figs. 14, 15. Pterid. Exsicc. Walter-Calle 42, Estonia (GH); Fig. 14. Spore with reticulate perine layer and projecting loops, × 860; Fig. 15. Basal reticulum and projecting loops, × 4400; Figs. 16, 17. Exsicc. Petrak, 702, Austria (GH); Fig. 16. Spore with reticulate perine layer and acuminate or looped projections (the commissural ridge is to the left of the center of the spore), × 1000; Fig. 17. Reticulum and echinate projections (several of these broken), × 4400.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high magnification, such as the broken processes near the top of the spore and ridge across the center of the New Zealand specimen in Fig. 18. The heavy coating at the base of the spore from Kashmir (Fig. 19) obscures the perine. The age and maturity of specimens are more critical factors in comparing the structural details of the perine layers. The photographs (Figs. 2-5) of portions of different spores of the same collection, at high magnification, show variations in perine deposition. Loss of the outer layer over much of the spore surface exposing the underlying exine layer in Fig. 5, seems to be a natural occurrence in var. *pubescens.* Erosion of this type may account for the frequent damage or loss of the perine layer in the process of acetolizing spores. The high percentage of smooth fern spores reported in studies of fossil material is probably also related to this condition.

A larger number of samples of material fixed in 85 percent lactic acid for two or more hours were examined with the light microscope. Immature sporangia, sporocytes and meiotic cells were also examined with the light microscope from material stained in aceto-carmine following fixation in 3:1 alcohol and acetic acid.

ACKNOWLEDGEMENTS

I am indebted to Dr. Thomas N. Taylor, University of Illinois, Chicago Circle and Robert G. Stolze, Field Museum, Chicago, for the SEM photographs noted above; and to F. N. Molea and G. R. Pierce, McKay Laboratory, Harvard University, for training on the Harvard instrument. For constructive comments on the manuscript, I am grateful to David S. Barrington, Umesh C. Banerjee, and especially to Rolla Tryon.

Figs. 18-22. Spores of *Thelypteris palustris* var. *squamigera:* Fig. 18. *Kirk*, Bay of Plenty, North Island, New Zealand (US), spore with diffuse echinate perine layer, × 1200; Figs. 19, 20. *Thompson*, Kashmir (GH); Fig. 19. Spore with echinate perine layer (looped projection at top right), × 860; Fig. 20. Echinate sculpture and basal reticulum, × 4400; Figs. 21, 22. *Drummond & Hemsley* 2187, Tanganyika (US), Fig. 21. Densely echinate spore, × 1000; Fig. 22. Echinate perine layer (basal reticulum at left of center), × 3200.

SPORE DEVELOPMENT AND STRUCTURE

Plants of var. *pubescens* studied, from Wisconsin, Maine and several from eastern Massachusetts, uniformly have 35 pairs of chromosomes at meiosis. Nuclear division precedes formation of the cell wall, resulting in four haploid sets of chromosomes within a single cell. At this stage, structural evidence of new walls or of cleavage was not observed. The walls which will partition the four cells in the tetrad become apparent at the same time. As the spores enlarge in the sporangium, in each tetrad they are aligned in a cruciform arrangement with the long axes of the pairs at right angles to each other. The convex surfaces of the spores become strongly curved as the cells enlarge and a gap develops in the center of the tetrad. When the spores are disassociated from the tetrad, a complement of 64 spores fills each of the sporangia. At this stage the spore walls are thick, and without special staining show dense granular organelles and plastids within the protoplast. Perine deposition is not evident on these thick walls, thus it appears that this material may be formed relatively late in sporogenesis. There is considerable variation in spore size within a sporangium in var. *pubescens* as some cells may be up to one-third larger than other well-developed ones.

In *Thelypteris*, the exine layer of the spore wall is sparsely textured in comparison with the outer perine layer, as shown in Fig. 5 and also at the top of the spore in Fig. 6 where the perine layer is broken. The gap between these layers clearly differentiates exine and perine stratification which composes the spore wall.

The work of Pettitt (1966) on ultra structure of *Asplenium Adiantum-nigrum* spores is helpful in interpreting spore wall structure in *Thelypteris*. The perine in *Asplenium* was shown to consist of four layers, two of them forming a raised sculptural pattern similar to that in *Thelypteris*. Two additional layers of perine in *Asplenium* are composed of more homogeneous material and conform to the contour of the subtending exine layer. This stratification suggests that the perine layer may be formed by a more

complex process than gelation, as discussed by Harris (1955). The structure of the perine layer in some species of *Bolbitis* has been examined by Hennipman (1970) and in this genus it was shown to consist of two well-defined layers. Sections through the sporangia in *Bolbitis*, with approximately mature spores, showed that the interstitial region between the spores was filled by a definite reticulum which was considered to form the outer perine layer.

The distinctive forms of perine sculpture shown in the geographic varieties of *Thelypteris palustris* suggest that the structure of this layer can be highly modified within a relatively closely related group. The series of photographs (Figs. 2-5) illustrates different development of the perine material in spores of a single collection of var. *pubescens*. The basis of some differences in the perine layers are shown at high magnification. The denser deposition in Fig. 4 represents additional material superimposed upon the coarser reticulated structure in Fig. 3. Evidence of similar subtending layers is often apparent in spores with outer verrucate or granulate perine layers, as shown in Figs. 10 and 11 of var. *pubescens*. The reticulate structure, shown in Fig. 3, is similar to that characterizing the outer perine layers in specimens of var. *palustris* from Europe (Figs. 14, 15) and of var. *squamigera* from Kashmir (Fig. 20). The verrucate material characteristic of the spores of var. *pubescens* and var. *Haleana* appears to represent an additional perine layer and these spores may represent a more derived form.

The marked differences in perine structure in the two species of *Bolbitis* studied by Hennipman were thought to reflect genetical differences which affect the interaction of haploid and diploid materials during spore formation. Differences shown in the perine layer of the varieties of *Thelypteris palustris* may represent structural adaptations of the spores to different ecological or climatic conditions in the evolution of these plants over their broad geographic range.

Studies on spore morphology at the ultra structural level, such as those by Heslop-Harrison (1968) on developmental

sequences in pollen, are critically needed for fern spores. The work on development and stratigraphy of pollen is applicable to spores. However, fern spores have a single nucleus and represent a simpler condition in comparison to pollen in which the microgametophyte has developed. In ferns, deposition of the external spore sculpture involves a tapetal periplasmodium, while in pollen of many higher plants a rigid cellular tapetum functions in wall formation. There are also differences in external forces which affect these structures. Fern spores are universally distributed by air, and there are no secondary agents such as insects, which are often involved in transport and influence the form of pollen in angiosperms.

MATURE SPORES OF THE VARIETIES OF THELYPTERIS PALUSTRIS

Spores of var. *pubescens* from Lexington, Massachusetts have a uniformly granulate or verrucate perine layer (Figs. 6, 7). The texture of this outer perine layer is considerably rougher than the subtending exine layer of the wall which can be seen at the top part of the spore (Fig. 6). In this variety the spores usually have a homogeneous perine layer with short, uniform projections. Some specimens, especially from the western part of the range, from Nebraska, Iowa and Illinois, have more irregular perine structure as seen in Fig. 8. At higher magnification (Fig. 9) the form of this perine is rougher but consists of papillate projections similar to those of spores from the eastern part of the range.

Spores of specimens of var. *pubescens* from Japan (Figs. 10, 11) usually have more prominent perine sculpture than the American material. These spores resemble the more strongly sculptured ones of the plants from the southern United States noted below.

Spores of var. *Haleana*, from Florida, have low, verrucate sculpture and some more prominent ridges as seen in Figs. 12, 13. Specimens from Bermuda have similar spores. The dense, relatively low, granulate or verrucate perine layers in this and the other mainly American variety are

basically similar, in contrast to those of the other two varieties of the Old World.

Spores of var. *palustris* from Europe, as shown by specimens from Estonia and Austria, have a strongly echinate perine layer, as shown in Figs. 14-17. The basal reticulum in these consists of prominent ridges encompassing large, irregular areolae, and projecting peaks or loops. The loops, shown at higher magnifications in Fig. 15, arise from the reticulum, and suggest that during the formation of this material a force is exerted on the strands, pulling them from the spore surface. The specimen from Austria has more prominently echinate perine and the detail of this (Fig. 17) shows several projections which are broken. The commissural ridge, at the left in the photograph of the whole spore (Fig. 16), appears to interrupt the reticulum. Spores of this variety from Finland (called *Lastrea Thelypteris*) were illustrated and described as having echinate perine by P. Sorsa (1964).

Spores of var. *squamigera* have prominently echinate perine as illustrated (Figs. 18-22). Loops may also occur, as shown in Fig. 19, and the lower reticulate layer with areolae and ridges is similar to that in spores of var. *palustris*. The spore surface of the Kashmir specimen, at higher magnification (Fig. 20), shows an aggregation of strands coalescent at the base of the projections. African specimens of this variety usually have denser and often more delicate projections as in Figs. 21, 22. Those from New Zealand have similar, but coarser and more diffuse, echinate sculpture (Fig. 18). New Zealand spores were illustrated by Harris (1955) and described as having a fairly regular papillate perine.

CHARACTERS OF THE VARIETIES OF THELYPTERIS PALUSTRIS

The concept of four varieties in *Thelypteris palustris*, proposed by Fernald, has been a useful one to indicate the geographic differentiation within the species. Exceptional variation in spore sculpture suggests that relationships may be more complex than shown in this classification. The principal characters used by Fernald to distinguish the

varieties were surveyed to determine possible correlation of these with the spores.

The condition of the veins of the fertile leaf was a major feature used by Fernald to distinguish the varieties. His comparison of venation was based on the number of simple or forked veins per segment. He reported veins as mostly forked in var. *palustris* and var. *Haleana* and simple in var. *pubescens* and var. *squamigera*. The present survey confirms these general trends. It also shows that a relationship exists between the condition of the veins and the size and degree of modification of the fertile lamina. Fertile leaves in var. *pubescens* tend to have simple veins and the leaves are more strongly dimorphic than in var. *Haleana* in which the veins are mostly forked. Several collections have been noted within the range of var. *pubescens* that have large fertile leaves with broad pinnae and with many forked veins (*Pammel* 579, Iowa; *Huett* from Ottawa, and *Geyer* from Beardstown, in Illinois; *Braun* from Kentucky). Generally, the Eurasian var. *palustris* has relatively large, fertile leaves with broad pinnae. The veins are usually forked, although some specimens with somewhat dimorphic leaves may have simple veins. Thus, fertile and sterile leaves in var. *palustris* and var. *Haleana* are more uniform in size and the veins are most commonly forked. Fertile leaves are modified in var. *pubescens* and var. *squamigera* and in these the veins are mainly simple, in contrast to the forked veins in sterile leaves.

Capitate glands on the indusia most readily characterize var. *palustris*. However, these indusial glands occur in some material of each variety. They are especially well-developed in collections of var. *Haleana* (*Correll* 5907) from Florida. In var. *pubescens*, specimens with glandular indusia such as *Clements*, Nebraska, are mostly from the western part of the range. Similar glands are abundant on the capsule faces of the sporangia in both varieties in eastern North America and are absent or rare on sporangia of the Old World plants.

Scales of the costa are particularly conspicuous in var. *squamigera* and provide the most useful character in dif-

ferentiating this variety. However, scales occur in some collections of each of the varieties. They are especially well-developed in some collections of var. *pubescens* from the western part of the United States (*Clements*, Nebraska). These scales are most abundant on the young leaves and may vary considerably in size. They persist on older leaves in var. *squamigera* and are more or less cauducous in the other varieties.

Some correlations are shown between other characters and variants in the spores, as noted above. However, the two basic forms of the perine layer — echinate in spores of plants from the Old World and verrucate in specimens mainly in North America — suggest new relationships within the species.

GEOGRAPHY

The present disjunct geographic distribution implies that the species may be a relatively old one. On the basis of its geographical area and adaptability to swamp life, Ching (1963) considered it archaic and a relict, possibly of the early Tertiary. Fernald regarded the species as having temperate rather than boreal affinities and suggested a tropical or subtropical origin. A boreal origin seems unlikely, as does a temperate one, during Pleistocene time, because of extensive glaciation over these regions. A tropical or subtropical origin during pre-Pleistocene time is regarded as more feasible. The New World tropics can be eliminated as a possible center since this region is remote from the current range of the species.

Continental southeast Asia is proposed as a possible early geographic center of the species, since three of the varieties now occur peripheral to this area, and the morphological diversity in the species is found largely among them. The arrows on the map (Fig. 1) indicate possible lines of geographic and evolutionary radiation from a southeast Asian center. The present range, which did not necessarily expand simultaneously in all directions, has undoubtedly been influenced by Pleistocene and post-Pleistocene environmental changes. The greater geographic disjunction in var.

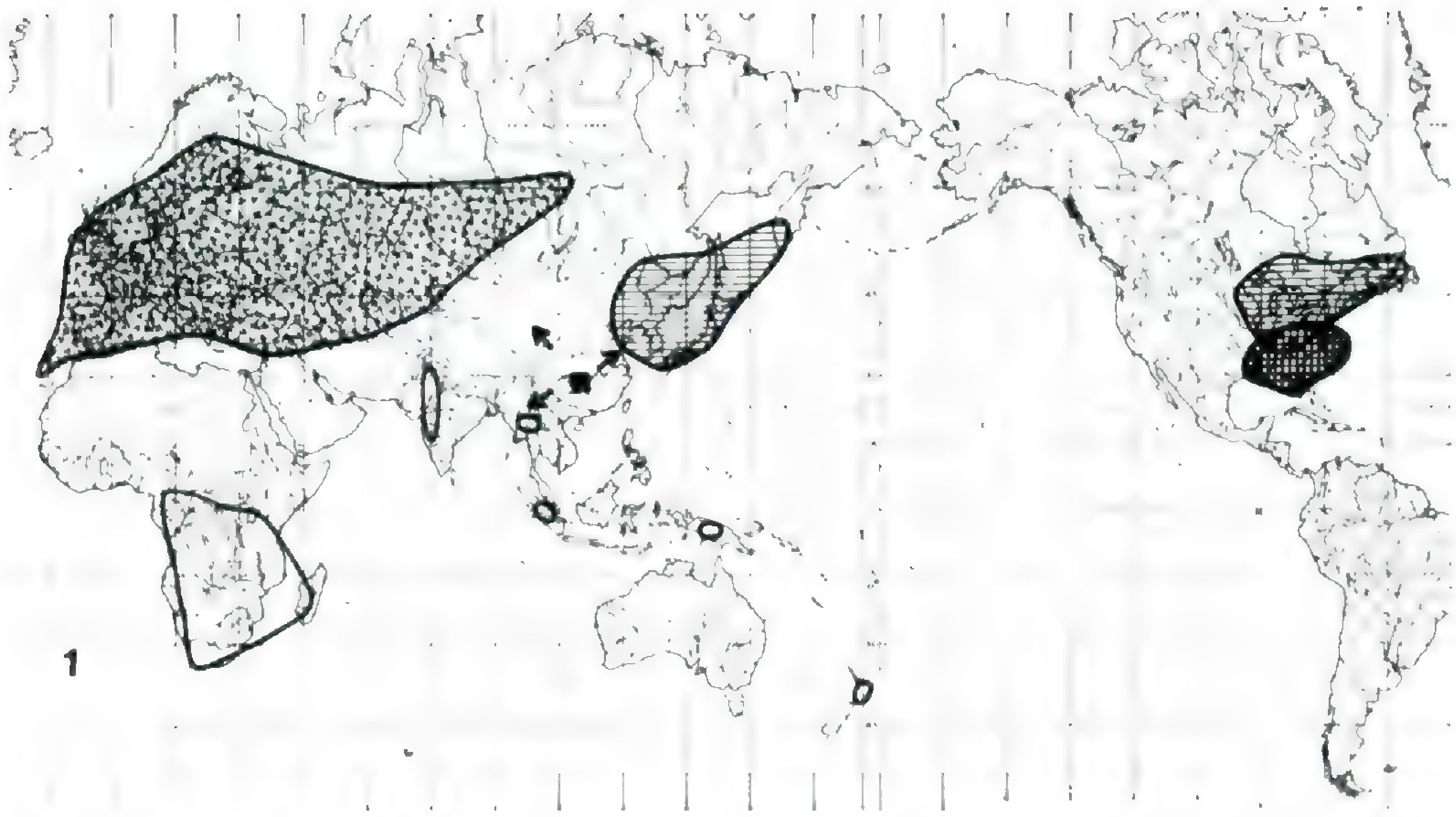

Fig. 1. Generalized geographic ranges of the varieties of *Thelypteris paustris* adapted from Hultén (1962): var. *palustris*, stippled; var. *pubescens*, horizontal lines; var. *Haleana*, vertical and horizontal lines; var. *squamigera*, elipses. The star represents a proposed central region of the complex with the arrows indicating radiation from it.

squamigera, for example, may reflect earlier range expansion and differentiation in that variety. The absence of plants in western North America and in much of southeast Asia may, in part, reflect the effects of Pleistocene glaciation in these regions. The wide geographic range may be accounted for in the evolutionary adaptations of the plants. Especially in the north, the range is correlated with the widespread regions of cool, wet climates with a dormant season.

The close relationship between the geographic elements of *Thelypteris palustris* in eastern North America and northeastern Asia is a familiar one in ferns. In these two regions, the same or vicarious species occur in *Camptosorus*, *Dennstaedtia*, *Diplazium* and others reported by Tryon (1970). Similar floristic relationships are shown by Li (1971) for many genera of flowering plants. The relationships, indicated by the spores, between the eastern North American and eastern Asian var. *pubescens* and var. *Haleana* in southeastern North America are of particular in-

terest and deserve additional attention. On the basis of the more modified fertile leaves with simple veins, collections from northeastern Asia are best placed with var. *pubescens.* However, the more prominently sculptured perine layer in the Japanese specimens show marked similarity to spores of var. *Haleana.* There are some differences between the spores from the western part of the range of var. *pubescens* in the United States and those of the east. The western plants, which also differ in scale and vein characters, may reflect relic populations of a less derived type or possibly represent more recent northward range expansion of populations of var. *Haleana.*

CONCLUSION

The survey of spores of *Thelypteris palustris* has shown new details of the wall structure and has revealed wide variation in the form of the perine layer. The variation is too great to permit species characterization such as is usually possible in ferns. These different patterns are attributed to adaptations of the plants as they have become dispersed over a broad geographic range.

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GRAY HERBARIUM

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PEUCEDANUM PALUSTRE AGAIN IN MASSACHUSETTS: On August 4, 1970 I noticed at the Great Meadows Wildlife Refuge in Concord, Massachusetts, a single large plant of an umbellifer at the edge of impounded water. I was unable to find it in the older manuals but was eventually able to identify it as *Peucedanum palustre* (L.) Moench. from Seymour's Flora of New England where it was based on one specimen in the New England Botanical Club's herbarium. This specimen collected in West Newbury, Essex County by S. K. Harris July 9, 1958 is apparently the first and only North American record of the species. (Rhodora **61**: 181). On August 15, 1970 I noticed about three dozen plants of this same species covering an area of about 20 × 40 feet in a damp meadow with *Eupatorium dubium, Solidago graminifolia, Sambucus canadensis* and *Onoclea sensibilis* beside a brook that flows into the Concord River a mile upstream from the Wildlife Refuge. The colloquial names are Marsh Hog's Fennel and Milk Parsley, the latter appropriate because of the milky sap that bleeds out when the stem is cut. The appearance of this colony over thirty miles from the discovery twelve years ago makes it seem probable that this species can be found in other locations in eastern Massachusetts, but has been overlooked by the

casual observer due to the similarity of its appearance to *Daucus carota* which has been so luxuriant and abundant this season. *Peucedanum palustre* is described and illustrated in Volume Two of John Hutchinson's BRITISH WILD FLOWERS (Penguin Books).

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VALIDATION OF REEDROLLINSIA WALKER (ANNONACEAE)

JAMES W. WALKER

In a recent paper dealing with the pollen morphology of the family Annonaceae (Walker, 1971), the author inadvertently published a new genus without a type species. I wish to rectify this oversight in the following note.

Reedrollinsia cauliflora Walker, gen. et sp. nov.

Flores cauliflori, pedunculus articulatus, cum bractea et supra et infra articulum. Sepala 4-5, in uno verticillo et basaliter connata, petala quoad numerum variabilia, pro parte maxima in verticillis duobus cum 4-5 petalis uterque, longa et ligulata, valvata, ad maturitatem marronina. Stamina peltata. Pollen inapertum. Ovula aliquot (ca. 4), lateralia.

Walker 357: GH (holotype); NY, US (isotypes).

This new genus of Annonaceae is named after my mentor and friend, Dr. Reed C. Rollins, Asa Gray Professor of Systematic Botany and Director of the Gray Herbarium of Harvard University. The single species is found in the state of Chiapas, Mexico. The specific epithet refers to the fact that the flowers are strictly cauliflorous.

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NOTABLE FERNS ON BEAR MOUNTAIN, HEBRON, NEW HAMPSHIRE. On July 2, 1969 Frederic Steele and I paid a first visit to Bear Mountain in Hebron having been impressed by its appearance on the topographic map, but more particularly by some prominent ledges on its southeastern side which we observed from a clearing. The southern slope of Bear Mountain is mostly a well developed hardwood forest with some stonewalls toward the base indicating earlier fields or pasture clearings. These are soon left behind on the upward climb and give way to a rich forest habitat of northern hardwoods with large trees of *Acer saccharum, Fraxinus americana, Betula alleghaniensis, Tilia americana* and even some fine specimens of *Juglans cinerea* below the ledges. The forest trees seemed to be somewhat unusual for west-central New Hampshire and also the character of lesser plants — the ferns and woodland herbs. There was an abundance of *Botrychium virginianum*, other Botrychiums, *Athyrium thelypteroides, Adiantum pedatum, Caulophyllum thalictroides, Osmorrhiza Claytoni, Carex plantaginea* and *Dentaria diphylla* and occasional plants of *Panax quinquefolius*. Earlier in the season *Dicenta Cucullaria* must be there in abundance as shown by scaly bases still in evidence. This attractive array of species prepared us in a sense for some interesting botanizing farther on.

We approached the ledges a bit too far to the west on this first trip to strike the richest habitats for ferns. We did however find some good specimens of *Cystopteris bulbifera* midway up the ledges and shortly thereafter encountered a few plants of *Dryopteris Goldiana* and *Polystichum Braunii* var *Purshii*. By this time we were tired after a full afternoon of plant hunting and were satisfied to have discovered three rare ferns, one of which, the Bulblet-bladder Fern, was well out of its New Hampshire range, the other two somewhat so. In fact, *Cystopteris bulbifera* is known from Coös County in townships that touch the Connecticut River, from Grafton County also near the River and in Sullivan County on calcareous ledges and in rich woods of the Connecticut Valley in the township of Plain-

field. *Dryopteris Goldiana* is reported by Seymour (1969) from Coös County, Lyman in Grafton County and Alstead in Cheshire County, all except the Alstead station being in northern New Hampshire. *Polystichum Braunii* var *Purshii* again is perhaps less disposed to inhabit calcareous soil but is northern in its New Hampshire distribution and in Hebron occurring at about its southern limit of range in the State.

In the summer of 1970 Steele and I instituted a fern trip to the area for the Audubon Society of New Hampshire but we failed to reach the "ledges" because we were too far to the west and the dense forest hid them from view.

It was my feeling that we had not yet exhausted the ferns of Bear Mountain. Consequently in late July of this year in company with Dr. William Yeo and my student, David Conant, I again attacked the mountain. This time we worked our way up the western side of the ledges to the top and after lunch and near catastrophe, occasioned by "yellow jackets" and a bad fall, descended gingerly to the base of the ledges on the eastern side where quantities of the *Polystichum*, *Dryopteris Goldiana* and *Cystopteris bulbifera* were growing luxuriantly all together amongst fallen boulders, at times carpeting them. While finding nothing new, we had by this time found a good place for a return trip. On August 7 I led the second annual Audubon Fern trip with every expectation of uneventfully climaxing the excursion with the visit to the base of the ledges. Everything went well; we found the anticipated ferns and began the descent from the cliff base through a particularly lush growth of fern fronds. To my astonishment, I soon found myself standing almost waist-high among fronds of *Athyrium pycnocarpon*, the narrow-leaved spleenwort. I had seen this before in Vermont but never in New Hampshire and of course realized it was a good find. Someone happily had brought along Edith Scamman's "Ferns of New Hampshire". We learned that this fern was known from Alstead in New Hampshire where it had been collected by Helen Noyes (later Mrs. Hollis Webster) and from Hanover where it was discovered by Mary Hitchcock. Specimens of her col-

lecting are present in the herbarium of the University of New Hampshire and in the Jesup herbarium at Dartmouth College, that at Durham bearing the date 1876. The Alstead station was reported by Helen Noyes (1900). A specimen presumably from there was collected by E. F. Williams in 1901 and is present in the New England Botanical Club Collection. Rugg (1948) discussed the Hanover occurrences for *Athyrium pycnocarpon* pointing out that the original Hitchcock station had apparently been destroyed but that a second locality for it in the northern part of Hanover had been discovered in 1943. The most recent specimen from this station in the U.N.H. herbarium was collected in 1947 by H. G. Rugg and J. P. Poole.

Specimens of the four species of ferns particularly discussed in this paper from Bear Mountain are deposited in the New England Botanical Club Herbarium (NEBC) and that of the University of New Hampshire (NHA).

I am in debt to David Conant for expert guidance to the "ledges" in Hebron on our most recent Audubon trip and for calling the article by Helen Noyes to my attention.

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Volume 73, No. 795, including pages 309-464, was issued October 15, 1971.

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Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Conducted and published for the Club, by

ALBION REED HODGDON, Editor-in-Chief

ALBERT FREDERICK HILL
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ROBERT CRICHTON FOSTER
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Vol. 73 September, 1971 No. 796

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The New England Botanical Club, Inc.

Botanical Museum, Oxford St., Cambridge, Mass. 02138

STATEMENT OF OWNERSHIP, MANAGEMENT AND CIRCULATION

Date of Filing: Nov. 15, 1971

Title of Publication: RHODORA

Frequency of Issue: Quarterly

Location of Known Office of Publication:
Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Location of the Headquarters of the Publishers:
Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Names and Addresses of Publisher, Editor and Business Manager:

Publisher:
New England Botanical Club, Inc., Botanical Museum, Oxford Street, Cambridge, Mass. 02138

Editor:
Albion R. Hodgdon, Dept. of Botany, Univ. of New Hampshire, Durham, N. H. 03824

Business Manager:
Herman R. Sweet, Botanical Museum, Oxford Street, Cambridge, Mass. 02138

Owner: New England Botanical Club, Inc., Botanical Museum, Oxford Street, Cambridge, Mass. 02138

No stockholders

Known Bondholders, Mortgagees and other Security Holders: None

	Average No. Copies each issue during preceding 12 months	Single issue nearest to filing date
Total No. copies printed	850	850
Paid Circulation		
Sales through dealers, etc.	none	none
Mail subscriptions	794	808
Total paid circulation	794	808
Free distribution		
1. Samples, complimentary, etc.	10	10
2. Copies distributed to news agents, but not sold	none	none
Total distribution	804	818
Office use, left-over, etc.	46	32
Total	850	850

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THE LEXINGTON PRESS, INC.
Lexington, Mass.

Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 73 December, 1971 No. 796

THE SYSTEMATICS AND ECOLOGY OF POISON-IVY AND THE POISON-OAKS (TOXICODENDRON, ANACARDIACEAE)[1]

WILLIAM T. GILLIS

(Continued from page 443)

ECOLOGICAL LIFE HISTORY

The bulk of scattered information about the natural history of *Toxicodendron* sect. *Toxicodendron* is here summarized as an ecological life history. The pattern followed is essentially a synthesis of the pattern of the Biological Flora of the British Isles format as published in the Journal of Ecology and the outline suggested by Pelton (1951). Inasmuch as most of the material relating to anatomy, morphology, hybridization, and taxonomy is included elsewhere, such material is not repeated; only additional topics will be discussed. Excluded from discussion is sect. *Simplicifolia* which includes only *T. borneense* about which virtually no data are available.

MORPHOLOGICAL LIMITS

Although the total length of time to elapse from the time of seed germination until the time a young plant can produce flowers is not known for all taxa, plantation studies of *Toxicodendron radicans* subsp. *negundo* have shown that three years were required for plants to progress from seed to flowering stage. The longevity of the species is unknown. However, trunks of *T. radicans* subsp. *negundo* are known

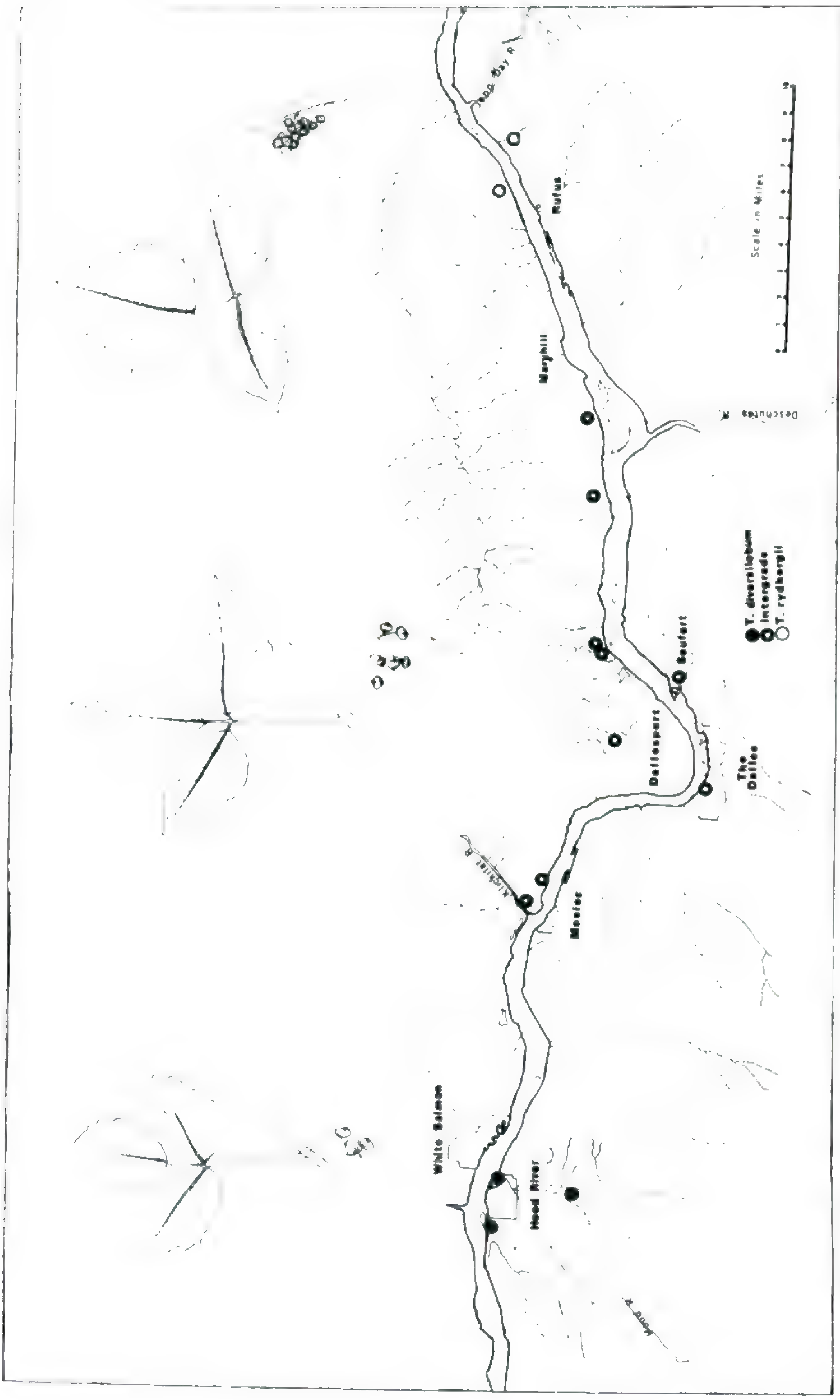


Fig. 53. Distribution of *Toxicodendron diversilobum* and *T. rydbergii* in the Columbia River gorge of Oregon and Washington and location of intergrades between them. (See text, page 423).

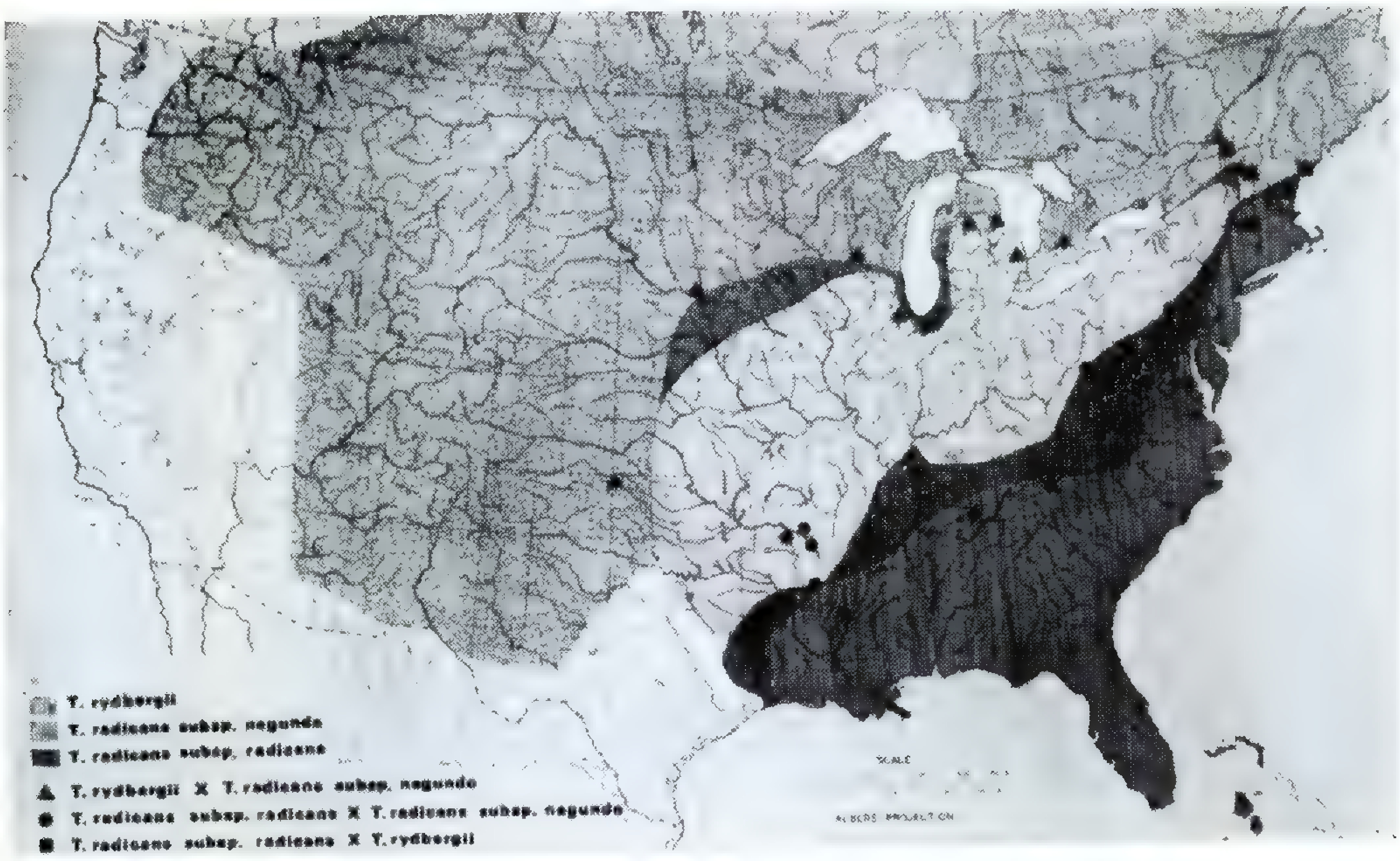


Fig. 54. Distribution of 3 taxa of poison-ivy in the United States and Canada and location of intergrades between them. (See text, page 436).

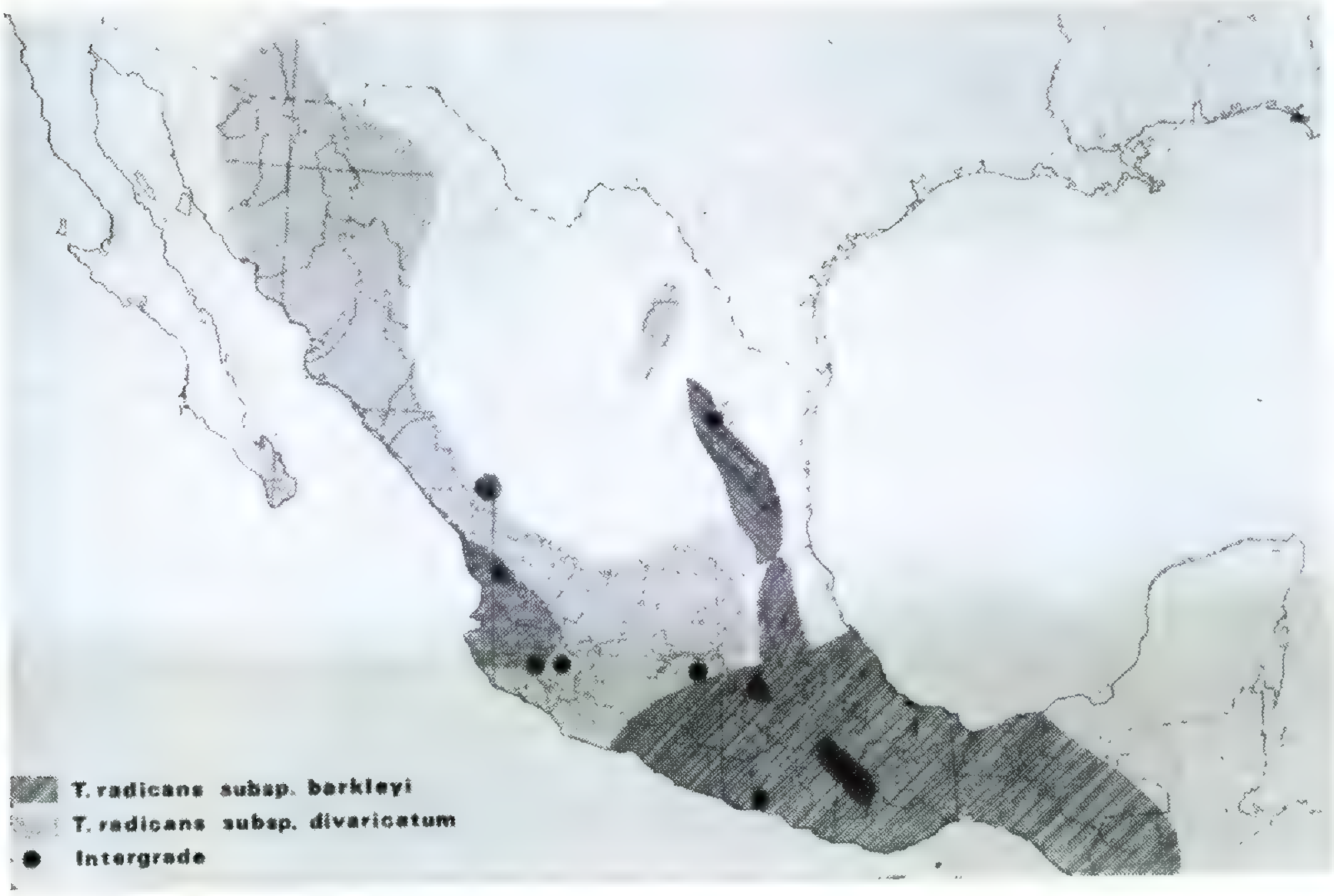


Fig. 55. Distribution of 2 taxa of poison-ivy in Mexico and location of intergrades between them. (See text, page 423).

up to 12 cm across, bearing 38 growth rings. The widely distributed collection of George Cooley (No. 2499) of *T. radicans* subsp. *radicans* from Sanibel Island, Florida, represents a tree of some five meters in height. This same individual tree is reported to have had a trunk diameter of 9 cm dbh, with one of its branches 13 dm long bearing 6130 flowers! (Cooley, 1955) Trunks of even larger *T. diversilobum* individuals have been reported in California.

ALTITUDINAL LIMITS

Data on elevation extremes for each species and subspecies are summarized in Table 15. The data come primarily from herbarium information. They are only approximate. Except for relatively high elevations, most collectors do not often record elevations with their collection data. A few additional remarks on altitudinal distribution from my own observations are perhaps in order.

In the Great Smoky Mountains *Toxicodendron radicans* subsp. *radicans* occurs at lower elevations but drops out of communities abruptly at 1070 m. Because of its abundance at elevations below 1070 m, the apparent scarcity above that elevation prompted a search for the plant at higher elevations, a search that proved fruitless. *Toxicodendron radicans* subspp. *negundo*, *pubens*, and *verrucosum* might grow at higher elevations if the requirements of soil, moisture, and community preference were satisfied there also. That is to say, altitude alone probably does not limit their distribution. Indeed, any upper altitudinal limit for these taxa probably is not reached anywhere within their natural ranges.

Toxicodendron radicans subsp. *hispidum* appears to be a true montane plant, having been collected nowhere at elevations less than 1150 meters. In Taiwan, where its distribution is better known than in China proper, it is restricted to the central mountains, and only at the higher elevations. In mainland China, it has been found at elevations estimated at 3450 meters at a latitude of about 25° N. It is perhaps these higher elevations which make the growing conditions more temperate at the lower altitudes.

TABLE 15. ELEVATION SPAN FOR SPECIES OF *TOXICODENDRON* SECT. *TOXICODENDRON*

T. radicans subsp. *radicans*	Sea level to 1070 meters (Smoky Mts.)
T. radicans subsp. *negundo*	Low elevations to 575 meters (Tuscarora Mt., Pa.)
T. radicans subsp. *pubens*	Low elevations
T. radicans subsp. *verrucosum*	Low elevations to 375 meters
T. radicans subsp. *eximium*	300-1700 meters
T. radicans subsp. *divaricatum*	Moderate elevations to 2500 meters
T. radicans subsp. *barkleyi*	Moderate elevations to 2800 meters
T. radicans subsp. *orientale*	Sea level to 1800 meters
T. radicans subsp. *hispidum*	1150-3400 meters
T. diversilobum	Sea level to 1500 meters
T. toxicarium	Low elevations
T. rydbergii	Sea level in Canada to 1150 meters in Oregon to 2500 meters in New Mexico
T. nodosum	Sea level (?) to 1500 meters

Toxicodendron radicans subsp. *orientale* is found at sea level in Hokkaido, but is rare at low elevations farther south, as in the Tokyo valley for example. In southern Honshu, it is more likely to be found in the mountains at moderate elevations. This taxon, however, does appear to have an altitudinal limit. In the Hakone and Nikko regions (35-37° N.) of central Honshu, where the plant has been collected most frequently, it is abundant at elevations of 1200-1300 m., but totally absent at 1800 m. In other words, for these taxa, there appears to be a relationship between latitude and elevation maximum such that the plants will reach higher elevations farther south in their respective ranges.

The relatively low Allegheny and Blue Ridge Mountains appear to act to some degree as a quasi-barrier to gene exchange, since *Toxicodendron radicans* subsp. *negundo* occurs west of these mountains whereas subsp. *radicans* grows east of them with some putative introgression in the mountains. Where *T. rydbergii* occurs in the Appalachians, it is found at the summits of mountains. Whether it is a relict there or is the result of recent invasion is difficult to assess. Where it has been found most frequently at higher elevations has been along road cuts, and it may well be expanding its range southward as habitats open up which satisfy the correct latitude-altitude coefficient.

Toxicodendron rydbergii probably reaches a true elevation limit that is caused by a complex of factors such as length of growing season, frequency of late or early frost, etc., factors which are associated with altitude. It is found no higher than 1150 meters in Oregon and Washington, but grows at elevations up to 2500 meters in New Mexico.

An attempt was made to calculate the coefficient of latitude-elevation maximum for *Toxicodendron rydbergii*, the only member of the species complex for which sufficient data are available to make such calculation. The determinations were based on highest known elevations for this species in Oregon and New Mexico, and checked by collections at high elevations from intermediate localities. The rela-

tionship between latitude and maximum elevation is a linear one whose formula is: $K_f = L\ (E_f + 12{,}000)$; where K_f = coefficient of latitude and maximum elevation when elevation is measured in feet, L = latitude in degrees north, and E_f = elevation in feet. Then, substituting for latitude and elevations, values in Oregon and New Mexico and elsewhere: $K_f = 7.2 \times 10^5$. Where elevation is measured in meters, the following holds: K_m = coefficient of latitude and maximum elevation when the elevation is measured in meters and E_m = elevation in meters. Then, again by substitution: $K_m = 2.18 \times 10^5$.

Daubenmire (1954) made a graph of altitude of timberlines in North America plotted against latitude and found a curve which was essentially linear for that part of the world between 35-70°. At more southerly latitudes, the curve changed markedly. For the range of latitudes involved in the distribution of *Toxicodendron rydbergii* (32-52° N.), the computing of a constant for maximum elevation should be more meaningful than for a spread from 0-70° N. Lat. It should follow a straight-line relationship, because the latitude span is all temperate. Furthermore, one is here concerned with the distribution of only one species, therefore involving a single niche, rather than that of an entire life form, i.e., forest trees. Daubenmire (*ibid.*) concludes that

> . . . along the main axis of the North American Cordillera, the elevation of alpine timberline rises steadily at a rate of about 110 m per degree of latitude between 60 and 30°, then declines very gradually to the equator.

Considering that his data include a variety of tree species and deal with highest elevations of species that live far higher than poison-ivy, it is interesting that the altitudinal maximum for *Toxicodendron rydbergii* also rises steadily at a rate of about 109 m per degree!

This close approximation to Daubenmire's figures suggests a biological value of some significance. The altitudinal limit of species distributions and its correlation with latitude might be explored for other plants and also for animals to see if the change of 109-110m/degree is approached.

FIRE

The plants of this complex generally occur in disturbed habitats which are likely to be disturbed repeatedly. The activities of man are important in creating this disturbance, but fire is also a major source of disturbance, especially for the forests in which *Toxicodendron toxicarium* is found. *Toxicodendron radicans*, *T. diversilobum* and *T. rydbergii* are plants which respond favorably to disturbance and are likely to become more abundant following fire, but I have no data to substantiate this supposition. For *T. toxicarium*, on the other hand, there are data to support this claim. In a stand of oak-pine in Lee County, Alabama, Auburn University Forestry Department maintains control-burn plots in which *T. toxicarium* is native. Sets of ten meter square random quadrats were examined in each of two stands — both burned and unburned. The number of shoots per square meter was recorded for each. For ten quadrats in the unburned area, the average was eight shoots/m^2; for ten quadrats in the burned area, the average was 26 shoots/m^2. At another site in Peach County, Georgia, where the most abundant Eastern poison-oak was found of any site investigated, there was ample evidence of burning a few years before (charred stumps, charcoal in the upper soil horizons, etc.). Fire, then, appears to enhance the abundance of *T. toxicarium*.

BIOLOGICAL INTERACTIONS

There are a number of interactions of poison-ivy and the poison-oaks with other plants and with animals. A number of these have been observed first-hand in the field, but most of the following references to such interactions have been derived from the literature. Where references have been consulted, attempts have been made to establish the taxon of *Toxicodendron* involved. Precision is not possible in most instances because the writers have failed to file a voucher specimen of the plant in question in any museum or herbarium, and/or the scientific name which may have been used has been a source of confusion, i.e., *Rhus toxicodendron.*

Among the parasitic fungi, two were found by Rhoads (1918) as examples of wound parasitism: *Polyporus gilvus* and *Irpex lacteus.* A rust genus, *Pileolaria,* is found primarily on *Toxicodendron* and *Rhus* species according to Dr. Joe Hennen (personal communication), having been found infecting *T. diversilobum* and a number of subspecies of *T. radicans* in herbarium material. Arthur (1934) claimed that *Pileolaria toxicodendri*[19] infects *T. radicans* throughout its range. Other fungal infestations are summarized in Table 16.

Insects and other arthropods work on *Toxicodendron* in a variety of ways. One of the chief pollinators of the poison-ivies in Michigan, the Carolinas, New Jersey, and the prairie states is the honey-bee *(Apis mellifera)*, which makes a non-toxic honey from its nectar. Presumably the honey-bee is a pollinating vector elsewhere, but has not been specifically recorded as such. Other visitors that appear to transport pollen included other Hymenoptera and

TABLE 16. FUNGI PARASITIC ON *TOXICODENDRON SPP.*

Polyporaceae	*Polyporus gilvus* (Schw.) Fr.	Rhoads, 1918
	Irpex lacteus Fr.	Rhoads, 1918
Pucciniaceae	**Pileolaria brevipes* Berk. and Rav.	Arthur, 1934 and Dr. Joe Hennen, personal communication
Melanconiales	*Cylindrosporium toxicodendri* (Curtis) Dearness	Schwarze, 1917

*Known to parasitize various North American subspecies of *T. radicans*, *T. diversilobum* and the Asiatic subspecies of *T. radicans*, subsp. *orientale* and subsp. *hispidum.*

[19]*P. brevipes* according to Hennen (personal communication).

several Coleoptera. A number of insect larvae have been observed eating the leaves, and indeed several have been reared to adult stages in the laboratory on leaves solely of this genus. Mr. Murray Hanna reared a nymph of *Clastroptera obtusa* on *T. radicans* subsp. *negundo* leaves in Okemos, Michigan. Dr. Roland L. Fischer reared larvae of *Arge sp.* to adult sawflies on the same taxon from Gull Lake, Michigan. From field observation, he noted damage to individual plants by this larva. Stripped leaflets on which only midribs remain are deposited as vouchers in the Michigan State University Herbarium (MSC). LeConte and Horn (1883) raised a dermestid beetle of the genus *Aspectus* from a tumor on a stem of poison-ivy. Mites were found in leaf galls on specimens of living *T. radicans* subsp. *divaricatum* brought from Mexico City, and determined by Mr. Robert Fouts of the Plant Quarantine Division of the USDA to be *Aculus toxicophagus* (Ewing).

Criddle (1927) observed that *Epipaschia zelleri* larvae made the leaves curl lengthwise to form tunnels. He claimed this larva was the most destructive of all insects to poison-ivy. Larvae of *Lithocelletis guttifinitella* tunnel into the petioles and leaves, making white circular cysts, notable especially as autumn coloration occurs. The pupae then overwinter in the leaves. From specimens deposited in the Michigan State University Entomology Museum, Mr. Julian Donahue has kindly furnished data to the effect that larvae of all members of the subfamily Eutelliinae (family Noctuidae) are known to feed on poison-ivy. Table 17 summarizes the known effects of insects on poison-ivy species.

Some birds eat the fruits of *Toxicodendron radicans* occasionally, and others eat them preferentially (Martin, *et al.*, 1951).[20] It is noted that various flickers, which are

[20]Although the species of *Toxicodendron* are not enumerated for each bird in the list, one can infer that references to the West Coast must be to *T. diversilobum*, Arizona to *T. rydbergii*, etc. There are certain references which cannot be pinned down precisely, e.g., New England.

fond of ants despite their formic acid content, are partial to fruits of *Toxicodendron*, its fruits comprising up to 25% of their diet. Barrows (1895) suggested that dissemination of the species was accomplished largely by crows. Certainly one may see birds of many kinds as being responsible for the seeds being dropped at the base of trees, telephone poles, and fencerows. There is some indication from anomalous germination tests that I obtained with disseminules of *Toxicodendron* species, that passage through an animal's digestive tract might be needed to break down the waxy and bony layers over the seed to facilitate germination.

Of mammals and their eating of Toxicodendrons, little is known. Although bears, rabbits, and mule deer have been observed browsing the plants (Martin, *et al., loc. cit.*), only the pocket mouse in California has been seen eating seed enough to comprise as much as 25% of the total diet. More than once I have heard of cases of dermatitis in human beings attributed to the skinning of rabbits or squirrels whose stomach contents were largely that of poison-ivy leaves and seeds. No experiments have yet been carried out to test this hypothesis, however. On the other hand, members of the poison-ivy complex are used by small animals in a way other than as food. In localities where ground cover is dense with *Toxicodendron radicans*, *T. rydbergii*, or *T. diversilobum* the cover and protection they afford are important contributors to the life of rodents which appear to be unaffected by the toxicity of the plants.

PERIODICITY

The flowering times, length of ripening periods, and earliest date of ripened fruits differ among *Toxicodendron rydbergii*, *T. diversilobum*, *T. toxicarium*, and the subspecies of *T. radicans*. Among the latter subspecies, there is some correlation of these periods with latitude. Dates discussed here are mean dates of maximum flowering and do not account completely for some precocious and some serotinous flowering. Whether late flowers are a response to photoperiod is not known. Early flowering never precedes the opening of new leaves.

TABLE 17. ARTHROPODS FEEDING ON *TOXICODENDRON SPP.*

LEPIDOPTERA		
Noctuidae	[1]*Paectes oculatrix* (Guenee)	Forbes, 1954, Kimball, 1965
	Eutelia pulcherrima Grote	Forbes, 1954
	[1]*Marathyssa basalis* Walker	Forbes, 1954
Lycaenidae	*Leptotes cassius* theonus (Lucas)	Morgan, 1933; Kimball, 1965
Pyralidae	[2]*Epipaschia zelleri* Grt.	Criddle, 1927
	E. superatalis	Hicks, 1952
Tortricidae	[1]*Episimus argutanus* (Clem.)	Hicks, 1952
	Cacoecia argyrospila Walker	Hicks, 1952
Nepticuliidae	*Nepticuli rhoifoliella* Braun.	Forbes, 1960
	Lithocelletis guttifinitella Clemens	Forbes, 1960
Gracilariidae	*Gracilaria rhoifoliella* Chambers	Forbes, 1960
HYMENOPTERA		
Argidae	[1]*Arge humeralis* (Beauv.)	Frank Craighead, personal communication

TABLE 17. — *Continued*

DIPTERA		
Cecidomyiidae	[3]*Lasioptera sp.*	Frank Craighead, personal communication
Cecidomyiidae	*Dasyneura rhois*	Felt, 1928
COLEOPTERA		
Scarabaeidae	*Phyllophaga ulkei* Smith	Howden, Howden, and Ritcher, 1951
Melolonthidae	*Serica vespertina* Gyllenhal	*ibid.*
	Diplotaxis bidentata LeConte	*ibid.*
Dermestidae	*Aspectus hispidus* Melsh	Hicks, 1955, LeConte and Horn, 1883
Chrysomelidae	*Pachybrachys tridens* (Melsh.)	MSU Entomology Museum data
Ipidae	*Pityophthorus rhois* Swaine	Frank Craighead, personal communication
Cerambycidae	*Astylopsis macula* (Say)	Beal and Massey, 1945
Cerambycidae	*Leptostylus albescens*	*ibid.*
Curculionidae	*Cryptorhynchus fuscatus* Lec.	*ibid.*
Scolytidae	*Xyleborus pecanis* Hopk.	*ibid.*

TABLE 17. — *Continued*

Scolytidae	*X. affinis* Eichh.	*ibid.*
Curculionidae	*Madarellus undulatus* (Say)	Blatchley and Leng, 1916
Scolytidae	*Hypothenemus toxicodendri* Hop.	*ibid.*
Scolytidae	*Pityophthorus consimilis* Lec.	*ibid.*
BORER	*Oherea ocellata* Haldeman	Frank Craighead, personal communication
Diaspididae	*Aspidiotis sp.*	McNair, 1923
Clastropteridae	*Clastroptera obtusa*	Murray Hanna, personal communication
Aphididae	*Carolinaia rhois* Tissot	Tissot, 1928
MITES		
Eriophyidae	[1]*Aculus toxicophagus* (Ewing)	Robert Fouts, personal communication

[1]Larvae on leaves.
[2]Considered by some to be the most destructive insect to the poison-ivy plant.
[3]Galls on aerial roots.

Time of flowering for *Toxicodendron radicans* subsp. *radicans* begins at the southern tip of Florida at some time between the end of January and the middle of February. The flowering date appears progressively later toward the north, arriving in late March and early April in northern Florida, mid-May in the Carolinas, early June in the middle Atlantic States, and the first week in July at the north-

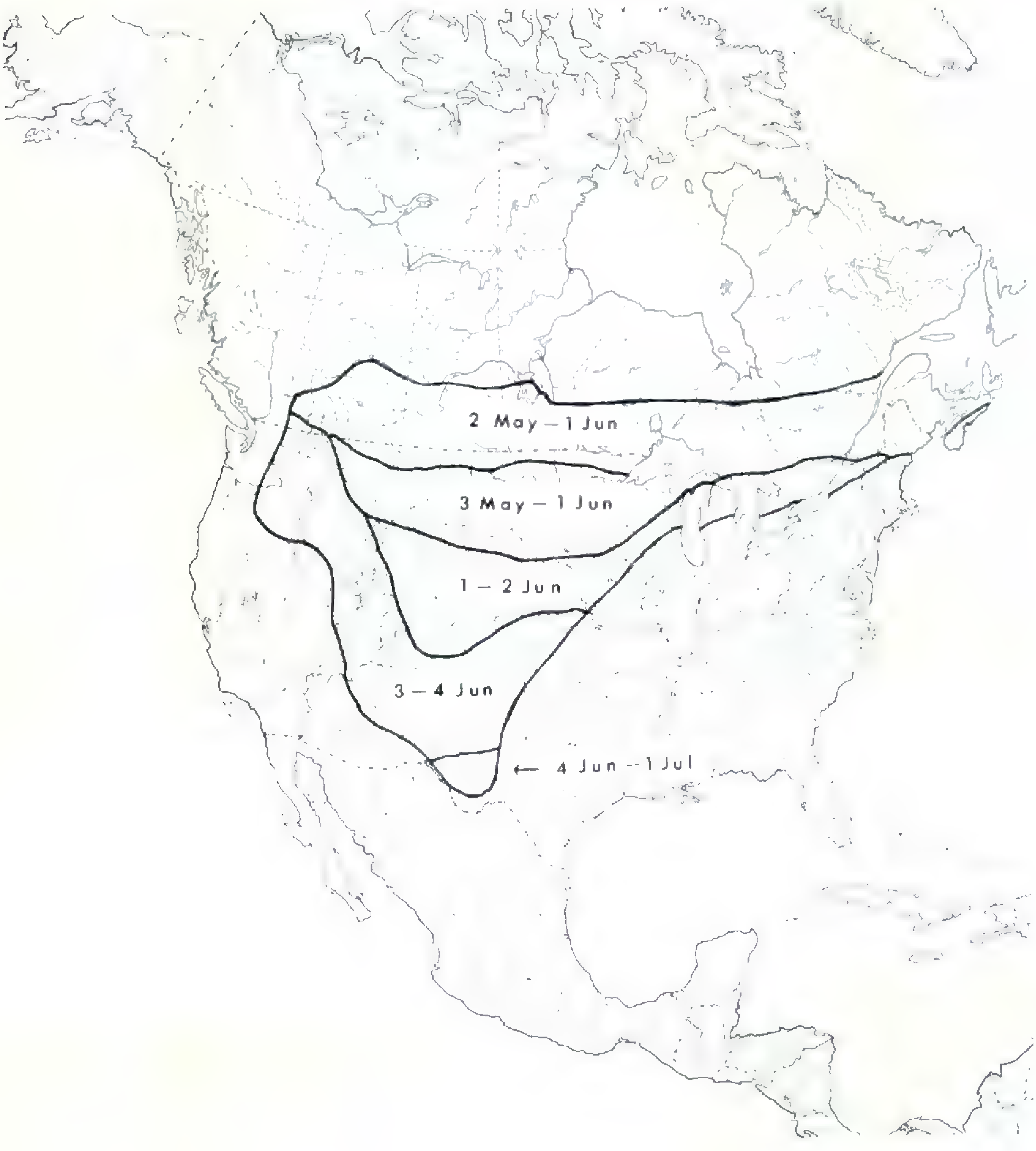


Fig. 56. Flowering periodicity of *Toxicodendron rydbergii*. Numerals refer to the *week* of the month in question.

ern limit of its range in southern Maine. Flowering periods for *T. rydbergii* begin the second week in May at the southern end of its range, and progress to the end of June and early July at its northern limit. For *T. radicans* subsp. *negundo*, the span is from mid-April to the latter part of June. Figs. 56 and 57 show the flowering date progression for these taxa.

Fig. 57. Flowering periodicity of *Toxicodendron radicans* subsp. *negundo*. Numerals refer to the *week* of the month in question.

In Japan, *Toxicodendron radicans* subsp. *orientale* flowers in late May in Kyushu and Shikoku, between the second week in June in southern Honshu to the first week in July for northern Honshu. In Hokkaido, the plant flowers during the last two weeks in June except for the Rishiri Islands, where it flowers early in July. In the Kuriles and Sakhalin, it flowers between the last week in June and the first week in August. Subspecies *hispidum* appears to flower in Taiwan at the end of April or in early May, and on the mainland of China during the last two weeks of May.

Within *Toxicodendron radicans* subsp. *divaricatum* there appear to be two periods of flowering maxima, one in April and May, and one in early to mid-August or even early September. There seems to be no geographical nor photoperiodic pattern to the flowering cycle. Even within a given area (e.g., Michoacán) flowering has been reported in early April, early May, early June, and late August from different populations. Further study might reveal correlations with rainfall or some other ecological factor, but for now, these differences are attributed only to local population variation. Subspecies *barkleyi* shows a similar spread of flowering dates, except that any secondary flowering period is earlier than that for subsp. *divaricatum* (early July rather than August or September). One Jalisco population, however, is recorded as flowering abundantly in November.

Flowering periods for *Toxicodendron diversilobum* shift northward with the season, beginning in late March in Baja California, commencing later in northern California and Oregon, and finishing the last week of May to the second week in June in Washington and British Columbia (Fig. 58). For *T. toxicarium*, on the other hand, a simple geographic pattern can be established. Fig. 58 also shows the flowering dates for this species.

Length of time required for fruits to ripen also differs with latitude for several taxa. For others, there are too few data to determine these figures precisely. Fruits are judged to be ripe when the exocarp is no longer green, no longer shrivels in the drying of herbarium specimens, and becomes brittle, separating from the mesocarp. At the

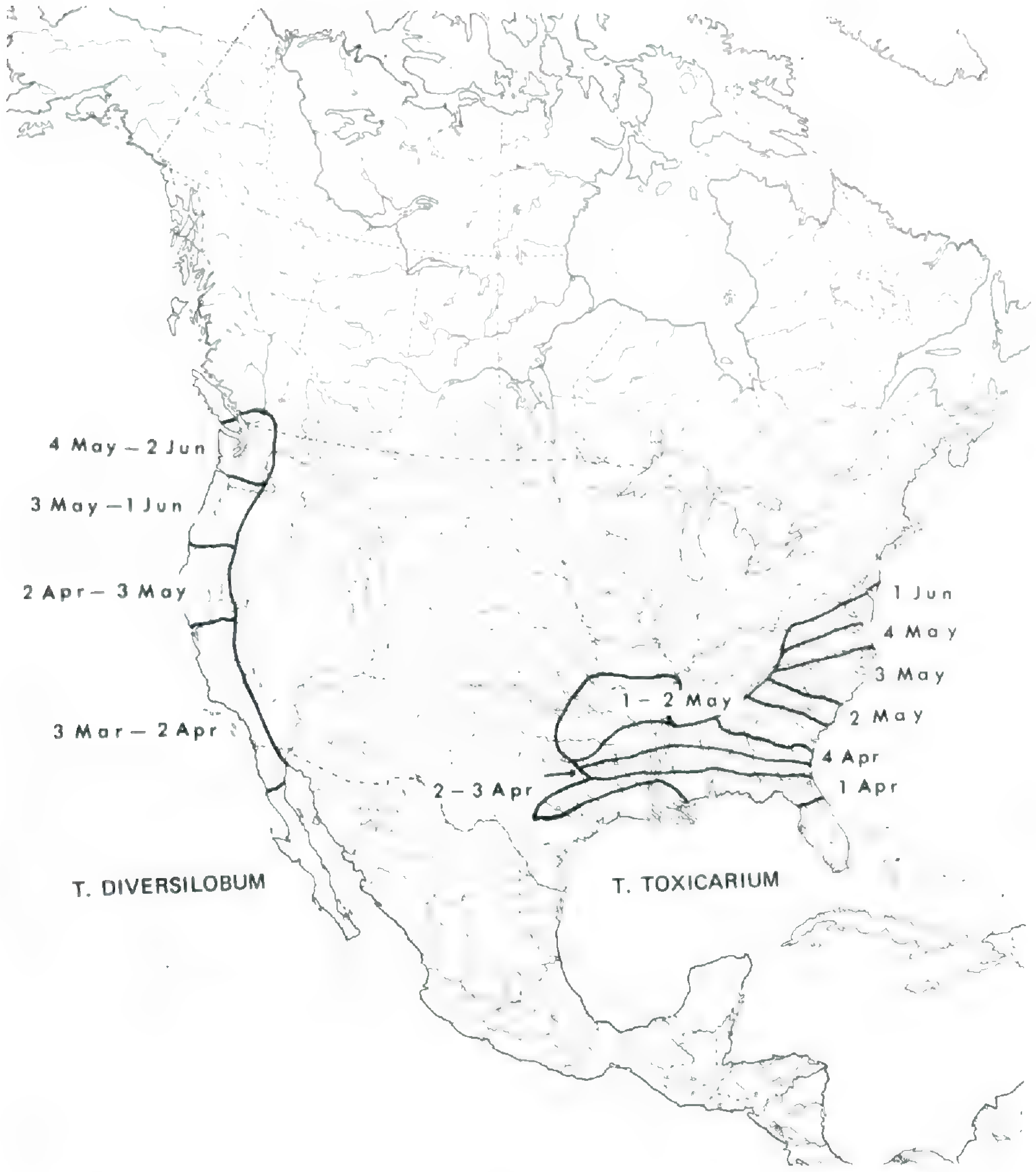


Fig. 58. Flowering periodicity of *Toxicodendron diversilobum* and *T. toxicarium*. Numerals refer to the *week* of the month in question.

southern tip of Florida, fruits ripen in *Toxicodendron radicans* subsp. *radicans* in three months, but in northern Florida, this ripening extends to four months. The ripening then shortens with increase in latitude to only two months in southern New England at the northern end of the range. Between central Florida and Maine, this average ripening difference is shortened by roughly four days per degree of latitude (Fig. 59).

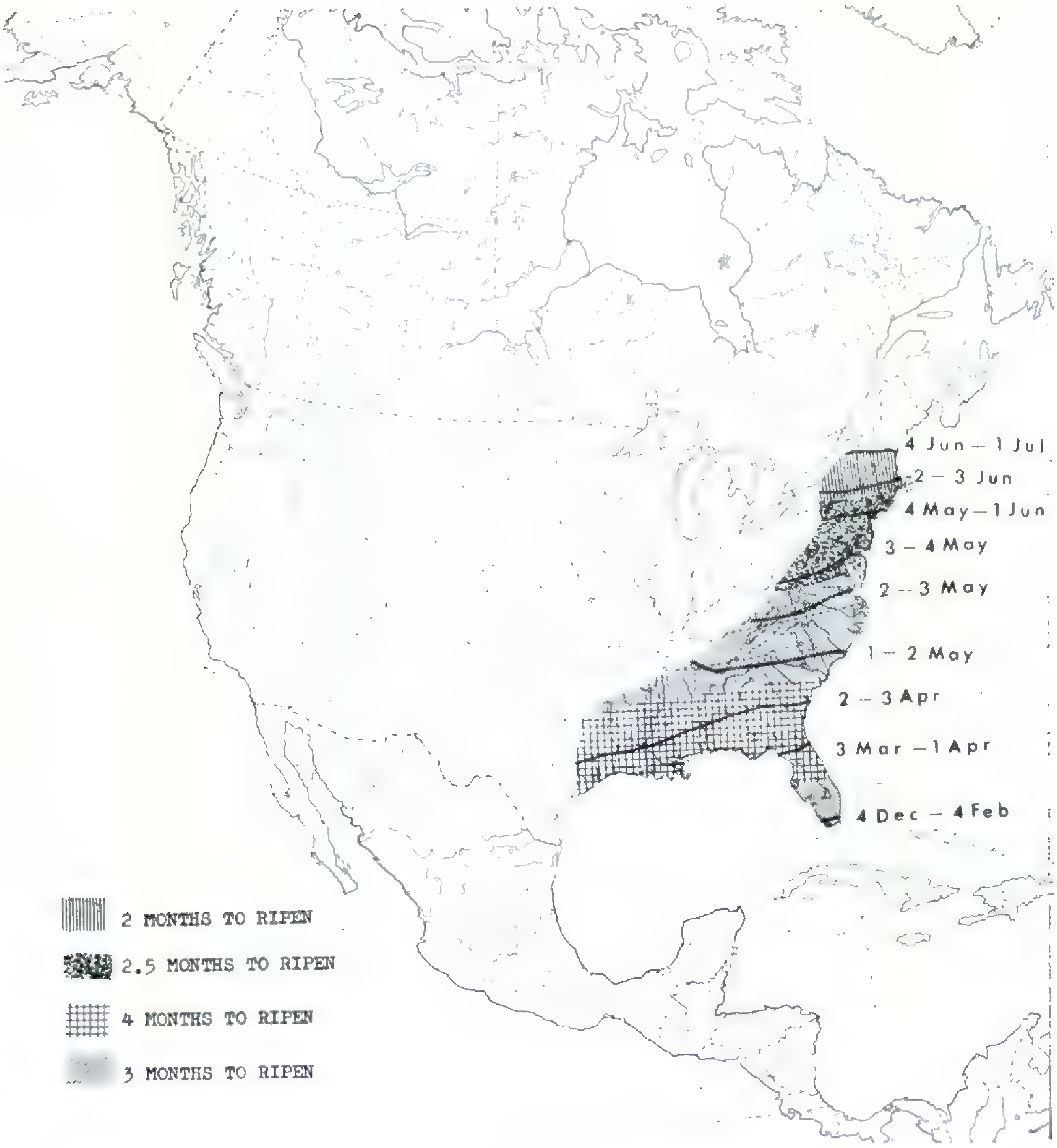


Fig. 59. Flowering and fruiting periodicity of *Toxicodendron radicans* subsp. *radicans*. Numerals refer to the *week* of the month in question. Shading refers to the length of time required for fruit ripening.

The span of latitude for subsp. *negundo* is smaller than that of subsp. *radicans*, so there is not so noticeable a difference in ripening time with changes in latitude. Throughout the range, except for upper New York (two months) and northern Texas (four months), the ripening time is about three months. Although extensive data are lacking for subsp. *orientale*, it appears that two months are re-

quired for ripening in Honshu, but only one and a half months in Hokkaido and north. No fruiting specimens from Kyushu or Shikoku have been seen.

Ripening of fruits of *Toxicodendron radicans* subsp. *divaricatum* requires about three months. The ripening time lengthens to four months in Baja California, and shrinks to two months in Sonora. Because of the divergence of flowering times, precise data for more than two or three localities were not obtainable. With what little data could be trusted from which to draw inferences about ripening time in subsp. *barkleyi*, it appears to require the longest period of all — up to four and a half to five months. Again from sparse data, one may estimate ripening time for subsp. *eximium* at one month, for subsp. *pubens* at three months, and for subsp. *hispidum* at two months.

Toxicodendron toxicarium requires from six to nine weeks for ripening of fruit, with no particular geographical pattern to the variations. *Toxicodendron diversilobum* requires eight to ten weeks for ripening with the shorter period in northern California north to Canada and the longer period in central California south to Baja California.

Toxicodendron nodosum has been collected more times in flowering stage than in fruiting condition. Flowering specimens have been collected from Java in July, August, and September, from Malaya in September (Larut) and December (Perak), and from Sarawak in June. Reliable ripening dates are not available, but what little data there are suggest that it takes about two months for the seeds to ripen.

In summary, one may say that the fruits of most members of the poison-ivy complex are ripe by the end of August or first part of September with three exceptions: (1) the early flowering (December to February) populations will be ripe by early summer; (2) the serotinous flowering populations will not produce ripe fruit until late in the calendar year if at all; and (3) *Toxicodendron nodosum* has different flowering and fruiting periods in different regions.

REPRODUCTIVE BIOLOGY

Most of the reproduction of poison-ivy and its allies is vegetative, enabling a single disseminule to grow to cover up to an acre of land. New populations, of course, are begun by seed. Cuttings do not fare well and are very susceptible to damping off. Only three cuttings grown in the laboratory (out of sixty-three attempted) were still alive three months later. None survived a winter out of doors in experimental plots in southern Michigan. These cuttings represented seven taxa (*Toxicodendron diversilobum*, *T. rydbergii*, *T. toxicarium*, *T. radicans* subspp. *radicans*, *negundo*, *divaricatum*, and *verrucosum*).

Germination is epigeal. The cotyledons are still borne within the tough endocarp and testa until after the hypocotyl emerges. A few never fully emerge, and die. The root hairs are brown. In those taxa wherein it was tested, viability is generally good to at least six years — no longer tests were run — but seeds require special treatment for germination.

A series of tests were set up to determine germination requirements. Seeds were gathered from 35 sources representing eight taxa. One hundred seeds of each population were placed in petri dishes on wet filter paper, replicated four times for each treatment. One treatment tested immediate germination without special treatment; another tested germination after six weeks of moist storage at 1° C. Results were tabulated up to four weeks after the start of the germination at room temperature, at which time the experiment was terminated.

Only seeds from populations of *Toxicodendron radicans* subsp. *radicans* in Gainesville, Florida, and in Bermuda germinated without after-ripening chill. No germination was recorded at all from seeds of *T. toxicarium*, *T. radicans* subsp. *barkleyi*; little germination occurred with seeds of *T. rydbergii*, *T. radicans* subsp. *verrucosum* and *T. diversilobum*. Germination results ranging from 10.75% to 62% were obtained for *T. radicans* subsp. *negundo*, and between 3.5% to 81.75% for *T. radicans* subsp. *radicans* (mean was

40%). Seeds produced during four seasons were gathered from one population of *T. radicans* subsp. *radicans* at Island Beach State Park, New Jersey (1955, 1956, 1958, and 1959). The average germination remained essentially the same, but appeared to increase very slightly with age. Table 18 gives the germination results. In order for conclusive growth studies to be possible in future experiments, the problem of germination must be solved, especially for the taxa for which no germination was effected. Scarification with acid, sandpaper, or fire, or removal of the mesocarp before testing were not tried.

TABLE 18. GERMINATION OF *TOXICODENDRON* SEEDS

Trials followed six weeks of moist storage at 1° C. Results are based on 100 seeds per trial and are recorded in per cent germination

	Replicate				Mean
	1	2	3	4	
T. radicans subsp. *radicans*					
Cape Hatteras, N. C.	27	43	54	46	42.5
Gainesville, Fla.	70	65	65	51	60.25
Chapel Hill, N. C.	17	10	19	21	16.75
Sapelo Island, Ga.	25	26	21	28	25.0
Bermuda	64	59	54	49	56.5
Williamstown, Mass.	13	29	21	16	19.75
Cape Charles, Va.	66	72	86	66	72.5
Middlebush, N. J.	95	72	77	83	81.75
Columbia, S. C.	4	6	3	1	3.5
Island Beach, N. J.					
1955	59	42	44	43	47.0
1956	21	29	35	39	31.0
1958	34	34	37	40	36.25
1959	33	36	34	29	33.0

TABLE 18. — *Continued*

	Replicate 1	2	3	4	Mean
T. radicans subsp. *negundo*					
East Lansing, Mich.	60	67	62	59	62.0
Haslett, Mich.	57	49	61	54	55.25
Norman, Okla.	10	14	10	9	10.75
T. radicans subsp. *verrucosum*					
Austin, Texas	1	2	6	3	3.0
T. radicans subsp. *orientale*					
Nikko, Japan	0	0	0	0	0
T. radicans subsp. *barkleyi*					
Galeana, Mexico	0	0	0	0	0
Huehuetenango, Guatemala	0	0	0	0	0
T. rydbergii					
Beulah, Mich.	0	1	1	0	0.5
DeTour, Mich.	0	0	0	0	0
Kah-Nee-Ta Hot Spring, Ore.	3	5	1	3	3
Saugatuck, Mich.	1	0	4	1	1.5
Lake Itasca, Minn.	0	0	0	1	0.25
T. diversilobum					
Berkeley, Calif.	0	0	1	3	1.0
Sacramento, Calif.	3	6	0	2	2.75
Placerville, Calif.	0	1	0	0	0.25
Trail, Ore.	1	0	1	0	0.5
Corvallis, Ore.	0	3	1	0	1
The Dalles, Ore.	0	0	0	0	0
Kalama, Wash.	0	0	0	0	0
T. toxicarium					
Morehead City, N. C.	0	0	0	0	0
Gaston, S. C.	0	0	0	0	0
Gainesville, Fla.	0	0	0	0	0
Bastrop, Texas	0	0	0	0	0

Seeds of a number of populations were weighed to determine if differences existed between taxa in seed weight. Fifty disseminules were weighed, each being an intact seed with endocarp and mesocarp attached. The total weights are tabulated in Table 19. The heaviest propagules are those of *Toxicodendron diversilobum*. Those of *T. toxicarium* and of *T. rydbergii* are next heaviest. Those of *T. radicans* subsp. *radicans* and subsp. *verrucosum* are the lightest. Putative hybrid "seeds" of *T. diversilobum* × *T. rydbergii* in the Columbia River Valley of Oregon were heavier than those of any pure species measured, averaging 2.38 g/50 seeds.

Community Specificity for *Toxicodendron Toxicarium*

The range of community types in which the various taxa of the poison-ivy complex grow is generally broad except for *T. toxicarium*. Other than for a very few unusual cases, its community preference is so marked that it can be readily spotted from a moving automobile. Its greatest abundance is in a sandhills type of vegetation typical of the Carolina fall-line sandhills, but common elsewhere on the Coastal Plain. This habitat may be described simply as a fairly open, dry, savanna woodland of oak and pine (more oak than pine). In Oklahoma and parts of Texas beyond the range of pine, most other components of the community are nonetheless present. The woods are usually disturbed, often by fire. They are never very old, generally less than fifty years. The wide spacing of the trees allows for a great deal of light to reach the herb layer where *T. toxicarium* grows. The soil is excessively drained; often the degree of dryness is emphasized by the presence of lichens such as *Cladonia cristatella* on the surface. The herb layer always has bunch and wire grasses: *Andropogon*, *Stipa*, or *Aristida*, and a variety of legumes: *Clitoria mariana*, *Petalostemon*, *Stylosanthes*, *Tephrosia*, and *Lespedeza* to mention a few of the more important. The acid litter of oak and pine has formed acid soils in which *Vaccinium* and occasionally *Gaylussacia* grow well. *Crataegus uniflora* and *Cnidoscolus*

TABLE 19. SEED WEIGHTS OF *TOXICODENDRON* SPECIES

Values recorded are in grams for fifty randomly-chosen seeds from a given population

Population	*T. rydbergii*	*T. radicans* subsp. *radicans*	*T. radicans* subsp. *verrucosum*	*T. radicans* subsp. *negundo*	*T. diversilobum*	*T. toxicarium*
1	1.14	1.2	0.83	0.97	1.77	1.40
2	1.38	1.71		1.17	2.05	1.70
3	1.34	0.53		0.90	1.54	1.57
4	1.20	0.55		1.45	1.64	
5	1.30	0.55			1.74	
6	1.22	0.75			1.63	
7	1.15	0.92				
8	1.52	0.92				
9	1.43					
Mean	1.297	0.891	0.83	1.12	1.728	1.56
Range	1.14-1.52	0.53-1.71		0.90-1.45	0.77-2.05	1.40-1.70

stimulosus are additional faithful components of this association. The general sandhills type of vegetation of which this association is a part has been described in detail by Wells and Shunk (1931) and Duke (1961). The Florida component of this formation is detailed by Laessle (1958) and Monk (1960). The chief associates of *T. toxicarium*, from my collections, are listed in Table 20.

Since the environments where *Toxicodendron radicans* is generally found are those which do not support *T. toxicarium*, an attempt was made to examine intensively the community preference for the latter to see what was specialized about its niche. A search was made for a habitat on the Atlantic Coastal Plain where both species grew close together and, if possible, grow in the same community. Two such communities were found that fit the objective well, plus a marginal third. These three are discussed herein and in the section on soils analysis.

One of the two major communities examined is in northern Florida in an area described as the San Felasco region about 12 miles NW of Gainesville in Alachua County (T. 9S., R. 19E., Sec. 21, 1.7 miles off Devil's Millhopper Road). It is best described as intermediate between hammock and sandhills vegetation and has been studied by Monk (1960) as he explored the transition between sandhills and hammock over a gradient of soil and vegetational change. An area of somewhat more than an acre was found near the site studied by Dr. Monk, in which both *Toxicodendron toxicarium* and *T. radicans* subsp. *radicans* grew together abundantly, i.e., an extensive tract of essentially transitional vegetation. The soils of the transition zone have a higher percentage of finer particles than the soils in which *T. toxicarium* generally grows, and are higher in calcium content than those where this species is usually common. On the other hand, it is probably the fine particles and increased calcium and other nutrients, especially in the upper soil horizons where the roots are concentrated, which enables *T. radicans* to survive. As Monk *(ibid.)* notes, this transition zone has species of both sandhills and hammock

TABLE 20. ASSOCIATES OF TOXICODENDRON TOXICARIUM IN SANDHILLS VEGETATION

	Georgia	Florida	Carolinas	Texas	New Jersey
Pinus palustris	x	x			
P. echinata		x			x
P. taeda	x	x	x	x	
Juniperus virginiana				x	
Myrica cerifera	x	x	x		x
Carya pallida				w	x
C. cordiformis			x		
C. tomentosa		x			
C. glabra		x	w		
Quercus alba					x
Q. falcata	x	x	x		
Q. incana	x		x		n
Q. laevis	x	x	x	w	n
Q. lyrata		x	x		
Q. marilandica	x		x	x	x

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Q. nigra		x	x		n
Q. stellata (incl. var. margaretta)	x		x	x	x
Eriogonum tomentosum	x	x	x	w	n
Polygonella americana			x		
Froelichia floridana	x	x	x	w	n
Magnolia virginiana			x		
Asimina angustifolia		x	x	w	
A. incana	n	x	n	w	n
Stipulicida setacea			x	w	n
Sassafras albidum		x	x		x
Crataegus uniflora	x	x	x	w	
Prunus caroliniana			x	w	n
P. umbellata		x		w	n
Aronia arbutifolia		x		w	
Rubus cuneifolius		x		w	

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
R. trivialis		x	x		
Baptisia leucantha		x		w	
Cassia fasciculata	x	x		x	
C. nictitans	x		x		
Centrosaema virginianum			x	x	
Clitoria mariana	x	x		x	
Crotolaria rotundifolia		x		x	
Desmodium canescens			x		
Galactia floridana		x		w	
Lespedeza hirta	x		x		
L. striata	x				
Lupinus villosus		x			
Petalostemon pinnatum	x			w	n
Phaseolus sinuatus	x	x		w	n
Rhynchosia simplicifolia var. tomentosum		x	x	w	n

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Stylosanthes biflora	x	x	x		
Tephrosia virginiana	x	x	x		
Polygala grandiflora	x	x		w	n
Cnidoscolus stimulosus	x	x	x	x	n
Croton argyranthemus	x		x		
C. capitatus	x		x		
Euphorbia corollata			x		
Stillingia sylvatica	x	x			n
Ceanothus americana			x		
Rhus copallina	x	x			
Ilex opaca		x	x		
Vitis cordifolia	x		x	w	
V. mustangensis var. linescumii				x	
Hypericum hypericoides			x		
Helianthemum georgianum	x	x			

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Lechea maritima	x		x	w	
L. villosa			x		
Oxalis dillenii		x			
Eryngium yuccifolium var. synchaetum	x				
Chimaphila maculata			x		
Gaylussacia frondosa			x	w	
G. dumosa			x	w	
Vaccinium arboreum			x		n
V. stamineum		x	x	w	
V. corymbosum	x		x	w	x
V. tenellum		x	x		
V. vacillans			x	w	
Polypremum procumbens	x				
Osmanthus americanus		x		w	
Gelsemium sempervirens	x	x	x	w	n

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Asclepias tuberosa	x	x			x
A. verticillata	x				
Phlox nivalis	x			w	x
P. floridana		x		w	
Callicarpa americana				x	n
Scutellaria integrifolia var. glandulosa	x	x		w	
Salvia lyrata	x	x			
Trichostema dichotomum					x
Penstemon australis		x	x	w	n
Verbena caroliniana		x		w	
Ruellia caroliniensis		x			x
Galium pilosum	x		x		
Diodia teres	x		x		
Berlandiera tomentosa	x	x		w	
Chrysopsis graminifolia			x		

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Elephantopus tomentosus	x	x	x	w	n
Eupatorium hyssopifolium	x		x	w	
Helenium tenuifolium			x	w	
Hymenopappus scabiosaeus		x			
Krigia biflora		x		w	
Pyrrhopappus carolinianus		x			
Senecio smallii	x	x	x		
Silphium compositum	x	x	x	w	n
Solidago brachyphylla		x			
S. bootii			x		n
S. odora			x		
S. tortifolia			x		
Tetragonotheca helianthoides		x		w	
Vernonia angustifolia	x	x		w	n
V. texana				x	

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Aristida lanosa	x			x	x
A. stricta	x	x	x	w	n
Andropogon scoparius	x		x	x	x
A. ternarius	x	x	x		x
Danthonia sericea			x	w	
Panicum potoricense			x		n
P. mutabile			x		
P. repens		x			
Cyperus retrofractus	x				
C. ovularis			x		
Smilax glauca			x	x	
Juncus secundus			x	w	
Nolina georgiana	x				
Polygonatum commutatum			x	w	
Sisyrinchium atlanticum		x			
S. fibrosum			x		n
Spiranthes grayi				x	

x = species collected, voucher deposited at MSC.
n = species reaches its northern limit south of New Jersey.
w = species reaches its western limit east of Texas.

communities, although some species which prefer extremes of each type are absent.

A clue to the ecological requirements of *Toxicodendron toxicarium* comes from a gradient study north of Columbia, Richland County, South Carolina (Fig. 60). A 110-meter transect was run along a 5% slope from a heavy textured soil where *T. radicans* subsp. *radicans* was frequent, to a sandhills community on sand where *T. toxicarium* was plentiful. Only in the middle of the transect did both species occur together, and there they occurred abundantly. Although the two plants flowered at the same time and had the same pollinating vector (honey-bee), there was evidence of only one individual which could be classed as a putative hybrid.

The vegetation analysis was made by selecting quadrats of ten meters on a side along the transect line, alternating sides of the base line. In these quadrats, all tree species were recorded in terms of diameter at breast height (dbh), and the measurements totaled for the quadrat. Two quadrats within the larger 100 m^2 quadrat were selected in which stems of all shrubs were counted. Four smaller quadrats were selected, nested within the 100 m^2 quadrats in which per cent cover of the plants in the herb layer was estimated. The tables which follow (21-23) show a gradual shift to the north from a hardwood forest to a sandhills oak-pine scrub, with lessening density of trees. Calcium content of the upper soil horizon drops and the soil texture becomes lighter; there is more leaching in the A horizon. Further, the species numbers become fewer. Loblolly pine occurs in each quadrat, but becomes less abundant (as do all tree species) upward along the gradient. In short, as measured up the gradient, the vegetation changes to one more characteristic of the typical vegetation in which *Toxicodendron toxicarium* may be found. Due to the plants' abundance, there is no lack of seed source for each extreme of the gradient to receive disseminules from the other end of the gradient. The differential in distribution of the taxa must involve factors in the soil and/or associated vegetation.

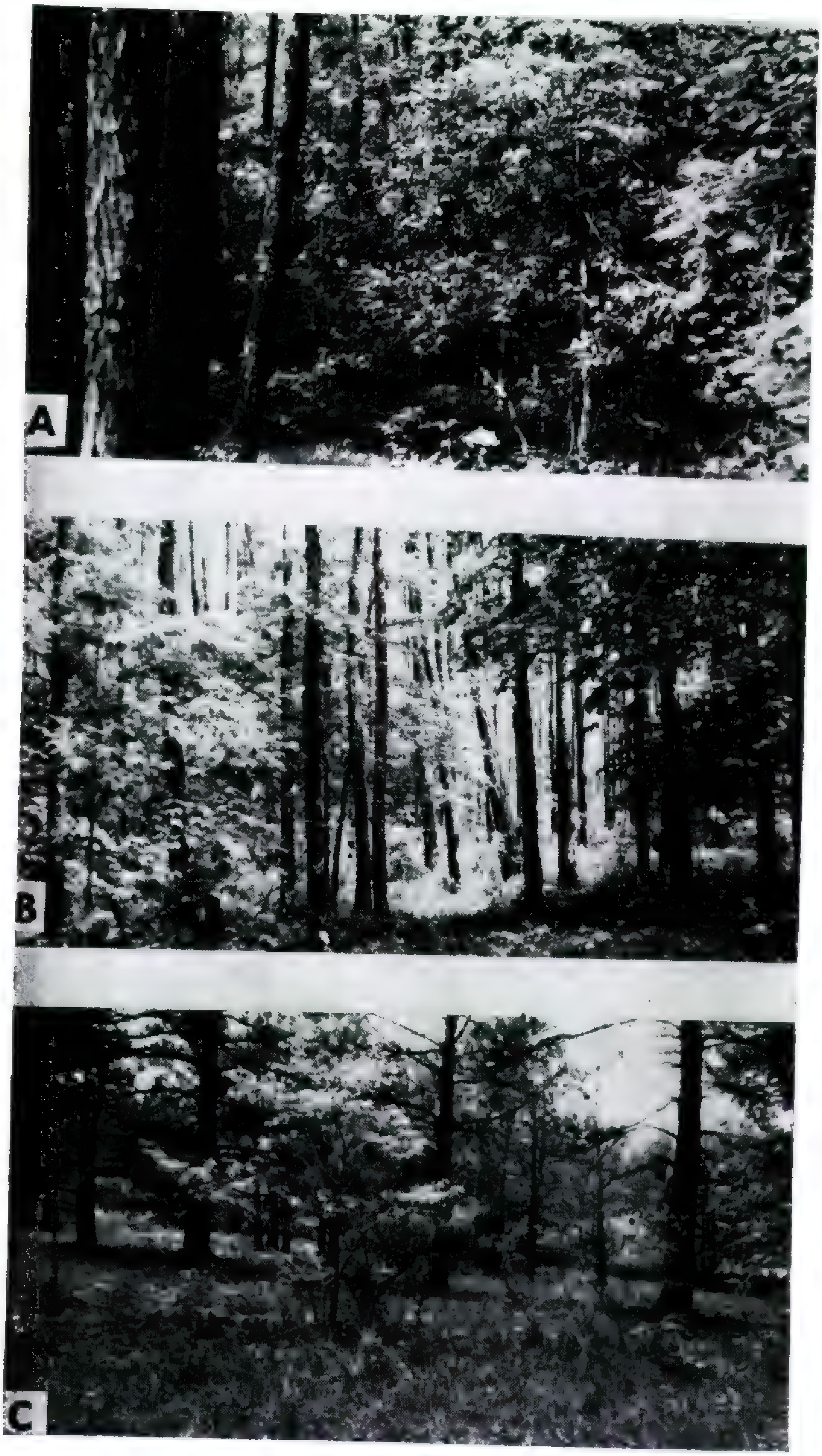


Fig. 60. Gradient through forest in South Carolina. A. View into mesic hardwood-pine forest on loamy sand. Poison-ivy is abundant. B. Middle of gradient where poison-ivy and poison-oak overlap. C. Dry end of gradient on coarse, shallow sand. Sandhills type of vegetation. Poison-oak is abundant.

TABLE 21. TREES FOUND ON TRANSECT FROM HARDWOOD FOREST TO SANDHILLS COMMUNITY, SOUTH CAROLINA. TRANSECT RUNS SOUTH-NORTH ALONG A DECREASING SOIL MOISTURE GRADIENT, COLUMBIA, RICHLAND COUNTY, SOUTH CAROLINA, 12 MAY 1961

Tree species are recorded if they occurred in 10 × 10 meter quadrats, and are totaled in dbh. for all trees within the quadrat and are expressed in sq. dm. Quadrat 1 is in hardwood forest; quadrat 10 is in sandhills vegetation

Species	Quadrats									
	1	2	3	4	5	6	7	8	9	10
Carya tomentosa	0.40								0.65	
Liquidambar styraciflua	0.05			0.08	0.45		0.14			
Cornus florida	0.08		0.31				0.30			
Pinus taeda	10.00	3.92	7.93	8.97	4.56	3.78	7.60	8.06	3.04	5.06
Acer rubrum		0.12		0.164						
Ilex opaca	0.1									
Quercus falcata		0.14								
Ceanothus americana	0.158			0.13						
Rhus copallina				0.06						
Quercus nigra						0.05				

TABLE 21. — *Continued*

Species	Quadrats									
	1	2	3	4	5	6	7	8	9	10
Prunus serotina							0.15		0.05	
P. caroliniana							0.11			
Quercus stellata						0.06				
Magnolia virginiana								0.05		
Quercus marilandica									0.90	

TABLE 22. SHRUBS FOUND ON TRANSECT FROM HARDWOOD FOREST TO SANDHILLS COMMUNITY, SOUTH CAROLINA. TRANSECT RUNS SOUTH-NORTH ALONG A DECREASING SOIL MOISTURE GRADIENT, COLUMBIA, RICHLAND COUNTY, SOUTH CAROLINA, 12 MAY 1961

Shrub species are measured by numbers of stems in 2 × 5 m quadrats, nested inside 10 × 10 m quadrats laid out for tree species measurements

Species	Quadrats										
	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a
Toxicodendron radicans											
subsp. radicans	7			1	2			6	31	19	7
Vitis cordifolia	32			4	14	2	27	21	19	11	16
Smilax rotundifolia	1							5	3	5	
Gelsemium sempervirens	2				3			2	2	3	2
Crataegus uniflora	2		2								
Acer rubrum		3	8						1		
Magnolia virginiana		3	8						1		
Vaccinium stamineum											
Smilax glauca			4		1		5	17			
Carya tomentosa			1					1			

TABLE 22. — *Continued*

Species	Quadrats										
	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a
Prunus caroliniana			1								
P. serotina				2		2			3		
Ampelopsis arborea				4	6	4	1				
Quercus nigra								1			3
Cornus florida								1			
Quercus lyrata								1	1		
Toxicodendron toxicarium								1		4	25
Rubus trivialis								2			
Quercus stellata									1		
Parthenocissus quinquefolia									3		
Rhus copallina											1
Quercus falcata											
Hypericum hypericoides											
Cassia nictitans											
Pinus taeda											
Vaccinium arboreum											
Liquidambar styraciflua											
Quercus marilandica											

TABLE 22. — *Continued*

Species	Quadrats										
	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a	11b
Toxicodendron radicans											
subsp. radicans	4	19	2								
Vitis cordifolia	12		2	2	2		11				
Smilax rotundifolia		1	2						2	4	1
Gelsemium sempervirens		5		2	8						
Crataegus uniflora	1										
Acer rubrum											
Magnolia virginiana											
Vaccinium stamineum	3				3	1	4	4	1	3	
Smilax glauca											
Carya tomentosa											
Prunus caroliniana		2	4	1	3		2	1		2	
P. serotina	2		2		1						
Ampelopsis arborea											
Quercus nigra	2		1						2		

TABLE 22. — *Continued*

Species	Quadrats										
	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a	11b
Cornus florida											
Quercus lyrata		1	4		4	1					
Toxicodendron toxicarium	6		4	2	8	5	3	16	18	11	19
Rubus trivialis			1								
Quercus stellata											
Parthenocissus quinquefolia	1										
Rhus copallina											
Quercus falcata	1	1									
Hypericum hypericoides	3	2									
Cassia nictitans	3										
Pinus taeda		2								2	
Vaccinium arboreum							3				
Liquidambar styraciflua							1				
Quercus marilandica							2				

TABLE 23. HERBS FOUND ON TRANSECT FROM HARDWOOD FOREST TO SANDHILLS COMMUNITY, SOUTH CAROLINA. TRANSECT RUNS FROM SOUTH-NORTH ALONG A DECREASING SOIL MOISTURE GRADIENT, COLUMBIA, RICHLAND COUNTY, SOUTH CAROLINA 12 MAY 1961

Herb species are measured by per cent cover in 0.5 × 2.5 m quadrats inside 10 × 10 m quadrats laid out for tree species measurements. t = trace, less than 1 per cent

Species	Quadrats											
	1a	1b	1c	1d	2a	2b	2c	2d	3a	3b	3c	3d
Vitis cordifolia	32	38	18	2	5	12	30	31	26	29	18	5
Gelsemium sempervirens	t	2	5	1	9	2	5	1	8	11	14	10
Silphium compositum	1	4	2									
Litter	60	65	75	80	70	85	66	75	65	63	51	85
Toxicodendron radicans subsp. radicans	9	4	3			1		1				
T. toxicarium	1	2										
Tree	3										4	
Rubus trivialis		t	t									
Poa sp.		t					t					
Magnolia virginiana			3									
Mitchella repens			t	t	t	t	1	3		2	1	1
Parthenocissus quinquefolia			2				t					
Acer rubrum				4	5	3						
Vacinnium tenellum				4	2							

TABLE 23. — *Continued*

Species	Quadrats											
	1a	1b	1c	1d	2a	2b	2c	2d	3a	3b	3c	3d
Smilax glauca				t	1		4			t	t	1
Carex sp.				t								
Senecio smallii					t							
Panicum mutabile				t		1						
Smilax rotundifolia						8	4			1		2
Lespedeza hirta						t6		1	1			
Quercus falcata						t						
Oxalis dillenii							t					
Prunus serotina								2				
Ampelopsis arborea									1	t	t	4
Euphorbia corollata								3	1			
Vaccinium stamineum											2	
Quercus lyrata											1	
Desmodium canescens												
Cornus florida												
Tephrosia virginiana												
Ceanothus americana												

TABLE 23. — *Continued*

Species	Quadrats									
	4a	4b	4c	4d	5a	5b	5c	5d	6a	6b
Vitis cordifolia	13	55	45	12	26	23	28	10	11	15
Gelsemium sempervirens	3	5	2	1	1	2	3	1	3	t
Silphium compositum										
Litter	80	36	50	70	60	64	62	67	60	40
Toxicodendron radicans subsp. radicans	t		1	2	5	31	25 =	11	2	t
T. toxicarium							13	7	19	38
Tree	t		15	1	4		2			
Rubus trivialis		1				4			1	
Poa sp.										
Magnolia virginiana										
Mitchella repens								4		
Parthenocissus quinquefolia			t	1	1	3	2			
Acer rubrum										
Vacinnium tenellum										
Smilax glauca	3	2	2	2	2	5	16	6	3	

TABLE 23. — *Continued*

Species	Quadrats									
	4a	4b	4c	4d	5a	5b	5c	5d	6a	6b
Carex										
Senecio smallii										
Panicum mutabile							1			
Smilax rotundifolia	2	t	2	6	7			1		
Lespedeza hirta										
Quercus falcata										
Oxalis dillenii										
Prunus serotina										
Ampelopsis arborea		2	2							
Euphorbia corollata										
Vaccinium stamineum										
Quercus lyrata		t								
Desmodium canescens		1								
Cornus florida			2							
Tephrosia virginiana							2		t	
Ceanothus americana										

TABLE 23. — *Continued*

Species	Quadrats											
	6c	6d	7a	7b	7c	7d	8a	8b	8c	8d	9a	9b
Vitis cordifolia	40	60	48	56	8	65	20	45	38	9	21	18
Gelsemium sempervirens	1	2	t	2	1	2	1	3	4	1	5	6
Silphium compositum												
Litter	45	25	26	24	85	80	60	45	45	78	60	60
Toxicodendron radicans subsp. radicans		3	7	6								
T. toxicarium	13				2	12	5			6	4	12
Tree	3	5	2	10			8			t		
Rubus trivialis						2			4	t	2	
Poa sp.												
Parthenocissus quinquefolia		3										
Smilax glauca			1	3			2					
Senecio smallii							1					
Lespedeza hirta	t		1	6								
Quercus falcata												
Prunus serotina												

TABLE 23. — *Continued*

Species	Quadrats											
	6c	6d	7a	7b	7c	7d	8a	8b	8c	8d	9a	9b
Stylosanthes biflora	1		t			3		1	3	2	t	1
Euphorbia corollata	t							1	2	1		
Ceanothus americana	2				t							
Pinus taeda		t		t	1		t					t
Quercus nigra		1					2					
Q. lyrata			5			1						
Desmodium canescens			8		1							
Polygonatum commutatum			2		1		t					
Galium pilosum				t	t	t						1
Danthonia sericea					t							
Prunus caroliniana					1			3		1		
Vaccinium stamineum						2		2				4
Tephrosia virginiana							t					
Quercus marilandica												
Andropogon ternarius												

TABLE 23. — *Continued*

Species	Quadrats									
	9c	9d	10a	10b	10c	10d	11a	11b	11c	11d
Vitis cordifolia	14	9	3	1		2				
Gelsemium sempervirens	5	12	3	4	2					
Silphium compositum	8		3				2			
Litter	70	55	30	65	88	90	75	75	92	90
Toxicodendron radicans subsp. radicans										
T. toxicarium	2		29	8	13	5		1		
Tree	t									
Rubus trivialis			2			1				
Poa sp.										
Parthenocissus quinquefolia										
Smilax glauca	4	30	11							
Senecio smallii			8	1	6	1	t	4	1	3
Lespedeza hirta	1						t			
Quercus falcata						2				
Prunus serotina										

TABLE 23. — *Continued*

Species	Quadrats									
	9c	9d	10a	10b	10c	10d	11a	11b	11c	11d
Stylosanthes biflora	t	1	3				1	1 =	t	1
Euphorbia corollata										
Ceanothus americana										
Pinus taeda							1			
Querycus nigra										
Q. lyrata										
Desmodium canescens										
Polygonatum commutatum										
Galium pilosum										
Danthonia sericea							t		t	
Prunus caroliniana	2									
Vaccinium stamineum		t		2	14		6	1		4
Tephrosia virginiana										
Quercus marilandica		13	2			1	11		2	1
Andropogon ternarius				t		t		t	1	t

SOIL STUDIES

A number of soil and site analyses were made to determine if members of the poison-ivy complex demonstrate any soil requirement specificity. A total of 38 soil pits was dug and samples of each horizon were brought back to the laboratory for analysis. These samples represented the soils in which nine taxa grew, of which four seemed to show some very specific requirements.

Each horizon was analyzed for texture, pH, and major nutrients available in parts per million. Soil texture was analyzed by the hydrometer method (Bouyoucos, 1936) and verified by touch. pH tests were run on a Beckman pH meter against a known phosphate buffer. The concentration of P, K, Ca, and Mg available was determined by the Soil Testing Laboratory of Michigan State University. From these data, soil profile information was synthesized and the profiles identified as well as could be done with available soil survey information. No soil data are available for the Asiatic taxa, except that it is known from herbarium label data that *Toxicodendron nodosum* has been found only on shallow limey soils. No data are available for the soils in which *T. radicans* subsp. *divaricatum* grows.

Although soil profiles were studied from a variety of sites where *Toxicodendron diversilobum* and the various poison-ivies grew, most of the common and widespread taxa occupy such a variety of habitats that the samples tell us little. The profiles which were examined demonstrate only a segment of the range of soil types in which these taxa grow: *T. rydbergii*, *T. diversilobum*, *T. radicans* subsp. *radicans*, *T. radicans* subsp. *negundo*, and *T. radicans* subsp. *pubens*. Even digging of soil pits would not be necessary to indicate that these plants will grow in a wide range of soils. They seem to be absent from podzols and heavily leached lateritic soils, however, and only rarely make incursions into peat. One taxon which seems to show narrow ranges of soil preference is *Toxicodendron toxicarium*; hence, this plant's soil requirements were examined more extensively.

Soil samples are of particular value from regions wherein several taxa form putative hybrids. If the parent taxa generally inhabit different kinds of soils, then a sample of the soil in which a suspected intermediate is growing may be used to complement morphological data to confirm the hybrid nature of the population. That is to say that the probability that the individual is a hybrid is increased if the individual appears to be growing in a soil that is also intermediate between the extremes preferred by its possible parents. Such samples have been used in corroborating the hybrid nature of populations of *Toxicodendron toxicarium* and *T. radicans* subsp. *radicans,* as will be shown later.

As one may note from collection record data, *Toxicodendron diversilobum, T. rydbergii,* and several subspecies of *T. radicans* generally grow well — and, in fact, reach optimum growth conditions — on floodplains. In those regions where the soils have been sampled also, individuals were climbing nearly every tree and formed a ground cover approaching 100% in the undifferentiated river alluvium. Such soils were determined to be an Underwood stony loam near Hood River, Oregon where *T. diversilobum* and the hybrid between it and *T. rydbergii* grew. The floodplain soil was a Genessee silt loam in East Lansing and Saginaw, Michigan, where *T. radicans* subsp. *negundo* was abundant.

The soil preferences for *Toxicodendron radicans* subsp. *negundo* were examined in a small study within Baker Woodlot on the Michigan State University campus for which a detailed soil map was available. The populations of poison-ivy were mapped for correlation with the soil patterns. To be sure, soils could not be adjudged to be the only factor operating to determine distribution patterns of the plant, but the conditions suggest that they are involved to a large measure.

Baker Woodlot (Ingham Co., East Lansing, Michigan. T. 4N., R. 1W., SW 1/4 Sec. 19) is probably a fragment of the forest that was cut over about one hundred years ago inasmuch as the oldest trees are about a century old. It is predominantly a beech-maple woods, but there are pockets

of other tree assemblages that appear to be related to soil substrate and soil moisture. *Toxicodendron radicans* subsp. *negundo* was expected to be common at the edge of the woods where light conditions would be more suitable than those inside the dense canopy, but it will be seen that some factor other than light must be involved in producing somewhat contrary data.

The "edge effect" is manifest on the east side of the woodlot where poison-ivy is found commonly. The soils in which the plant is growing have a medium to high natural fertility and moderate to high available moisture. On the south side of the woods there is little poison-ivy despite an improved light regime from that inside the woods. The south side is clearly disturbed. It serves as a railroad right-of-way, was clear-cut long ago and planted with pine and locust. For the most part, the soils which occur on the south side are — with the exception of Miami loam, one of the better agricultural soils of the state — poorly drained with low natural fertility and with low or variable moisture available for uptake. Such soils are Coloma loamy sand, Hillsdale sandy loam, Locke sandy loam, Berrien sandy loam, Granby loamy sand, Carlisle muck, and the Washtenaw soil. Poison-ivy is likewise uncommon along the west and north edges of the woods. In the northwest corner is a patch of Spinks loamy fine sand which supports a tangle of brambles, gooseberries, and trees, but no poison-ivy. The area is lower than much of the woods and supports a vegetation that is fairly open to light. Presumably it is the low fertility which has precluded its supporting any population of poison-ivy.

Perhaps this analysis of a single woods, its soils, and its poison-ivy population can form a generalization about *Toxicodendron radicans* subsp. *negundo* and its soil requirements. Contrary to popular opinion, poison-ivy is not ubiquitous, but rather requires fairly rich soils. It is all but missing from soils which are low in fertility, or in available moisture, and does not generally grow in standing water. Whereas the plant generally was found to be uncommon on the poorly drained Wauseon soil (composed of a two-storied

parent material: a fine sandy loam to loamy fine sand on top of a clay loam to silty clay loam till lower story), it was abundant on this soil surrounding a muck patch in the northern center of the woods. This abundance is presumably attributable to edge effect (border of an open *Cephalanthus* community), to increased fertility, and to the greater drainage afforded by the increase in slope. Poison-ivy thus appears to grow best in soils of high nutrient value and good, but not excessive, drainage.

From the soils sampled for *Toxicodendron rydbergii* populations, it appears that this species generally inhabits slightly more alkaline soils than does *T. radicans* subsp. *negundo. Toxicodendron radicans* subsp. *radicans*, from similar types of soils studies, appears to inhabit slightly more acid soils than either of the taxa mentioned above. Both of these generalizations are admittedly oversimplifications, especially in view of the fact that only six profiles were examined for *T. rydbergii* and five for *T. radicans* subsp. *radicans*.

When one considers the broad geographical sources of these soil samples (New England to the Pacific Northwest and to Florida), the data assume a greater significance despite their apparent skimpiness. In examining the soil profiles for those sites in which *Toxicodendron radicans* subsp. or *T. diversilobum* were found, the A horizons of the soil — and to a lesser extent, the upper B — seem to be the most significant in determining growth conditions for the plant, for it is in the A where maximum root development takes place. Only occasionally do roots penetrate to the B horizon, and then only in the upper B. It is perhaps for this reason that *T. radicans* is virtually absent from well-developed podzols or laterites wherein the A horizon is highly leached of minerals, especially Ca and Mg.

A study was made to determine the mineral nutrient requirements for poison-ivy. Seeds of various taxa were germinated on filiter paper in petri dishes and then transferred to a series of hydroponic solutions. Seedlings were grown in complete nutrient solution as a control, and in a series of solutions lacking respectively Ca, Mg, P, K, Fe,

N, and S. Four replicates, involving different taxa each, were carried out in the greenhouse. After two months, the experiment was concluded and evaluated.

Seedlings grown in complete nutrient solutions progressed well. Those grown in Mg-poor solutions initially performed poorly and dropped all leaves, but axillary buds developed and the plants were relatively healthy at the end. Furthermore, plants grown without Mg developed the longest roots. Except for Ca, no one mineral nutrient seemed entirely crucial. Absence of Fe produced mottling on the leaves and some chlorosis; absence of NO_3 resulted in chlorosis, etc. In Ca-poor solutions, however, the most marked effect of all resulted. The seedlings did not develop beyond the cotyledon stage before they died. Even though no tests were run to determine at what minimal concentration calcium becomes critical, it appears safe to say that calcium is the most important of the elements tested in the soil for the growth of taxa in the poison-ivy complex.

It was noted earlier that *Toxicodendron rydbergii* has generally been found growing in soils with fairly high concentrations of calcium. In agricultural sites, these soils would be described as not requiring additional lime to support good growth of most common crops. *Toxicodendron diversilobum* has been found in soils with similar Ca concentrations — none analyzed yielded less than 230 ppm of Ca. For *T. radicans* subsp. *verrucosum*, only one soil was found in which the significant concentrations of calcium were below 350 ppm in those horizons in which roots were found. At this site (Harrison County, Texas, east of Marshall), soil calcium in the A and B horizons ranged from 98-231 ppm. Here, poison-ivy was rare, found only with difficulty after a long search, probably because it was at the lower limit of its calcium requirement. Furthermore, *T. radicans* subsp. *verrucosum* has its main distribution on the limestone and dolomite Edwards Plateau and Arbuckle Mountains, where soils are naturally high in calcium.

Only once was *Toxicodendron radicans* subsp. *eximium* studied in the field, in the Chisos Mountains of the Big Bend region of Texas. It was growing in a lithosol on

basalt. The calcium content of the soil was determined to be 1099 ppm. The soil in which one population of *T. radicans* subsp. *barkleyi* grew at the edge of an orchard in Galeana, Nuevo Léon, Mexico, was sampled and examined critically in the laboratory. Here the soil calcium was higher than that for any other soil studied, namely, up to 5700 ppm.

For *Toxicodendron toxicarium*, the soil regime is very different. Unlike any other taxon in this complex, it grows in podzols at its northern limit (Lakewood sands in southern New Jersey), but otherwise is mostly confined to well-developed lateritic soils of the red-yellow podzolic great soil groups, both types of soil having a strongly leached A horizon and a well-developed layer of illuviation in the B. The soils are chiefly light textured, at least in the A and B horizons, where maximum root development takes place. They are moderately to strongly acidic, and uniformly have very low concentrations of Ca. Of the nine soil samples from *T. toxicarium* habitats, sampled from seven states throughout the range of the plant, the highest calcium content was found in the B_1 of a loamy sand in Bastrop State Park, Texas (91 ppm) (Fig. 61). The parent material of this soil contained far higher Ca concentrations, but was out of reach of normal root development. Interestingly, there was no *T. radicans* found there. Most soils which were tested in which *T. toxicarium* grew had far lower Ca, even down to 9 ppm. To some extent, K concentrations were also impoverished.

All of the soils in which *Toxicodendron toxicarium* is indigenous have developed under acid-forming litter, thus leading to heavy leaching. Scrub oaks are dominant with pine a usual constituent in this kind of woods except in the western end of the range of *T. toxicarium*. Drainage of the soil is high to excessive. Such soils are the Lakewood sand, a podzol, and the Lakeland sand, Norfolk sand, and Stephenville fine sandy loams, lateritic soils. The differences in these soils are in parent material, extent of horizon development, and thickness of sand over heavier sediments. The Lakeland, Lakewood, and Norfolk sands have

Fig. 61. Road cut in Bastrop County, Texas showing profile of soil in which *Toxicodendron toxicarium* is abundant.

developed on unconsolidated acid sands of the Coastal Plain; the Stephenville series has developed over parent materials derived from reddish sandstone or interbedded sandstone and sandy shale. The latter was the one soil sampled for a poison-oak habitat that was off the Atlantic or Gulf Coastal Plains (in Oklahoma).

The Lakeland soils show little profile development, chiefly because of the low clay content of the parent material, lacking the finer textured subsoils of the Norfolk and Lakewood series. The Norfolk, Lakeland, and Lakewood series differ in that there is a greater thickness of sand over heavier sediments in the Lakewood and Lakeland than in the Norfolk. There are generally heavier textured upper soil horizons in the Norfolk than in either other series. Suffice it to say that all of these soil series have much in common, despite minor differences in profile development. The physical and chemical attributes of the root environment are appreciably similar. No collections were made from any soils determined to be the Orangeburg, a major soil of the Carolina sandhills according to Duke (1961).

Although poison-ivy (*Toxicodendron radicans subspp.*) may inhabit sand dunes and the coastal plain sands, it is not indigenous to the poor soils of the sand scrub as is Eastern poison-oak (*T. toxicarium*). *Toxicodendron radicans* appears to grow in soils that have a higher Ca and usually higher Mg content than the ones in which *T. toxicarium* grows. Furthermore, *T. radicans* generally grows in heavier textured soils than *T. toxicarium*, with less leaching in the A horizon.

Several areas of transition between soil types and corresponding vegetation have been studied where both *Toxicodendron radicans* subsp. *radicans* and *T. toxicarium* were growing intermixed. One area is a gradient along a 5% slope between a Norfolk loamy sand (thin solum phase) and a shallow, incipient Lakeland sand north of Columbia, South Carolina. There is abundant poison-ivy at the lower end of the slope in a heavy-textured soil, poison-oak at the upper end in a shallow coarse sand, and both in the middle of the zone described in greater detail in the section of

this paper on Community Specificity for *T. toxicarium* (Fig. 62). A second plot that was studied is in an extensive area of essentially transitional zone between a mesic hammock community and a sandhills community in the San Felasco region of Alachua County, Florida. A third area where poison-ivy was found in association with Eastern poison-oak was in an oak-pine woods in Lincoln County, Mississippi (T. 7N., R. 7E.).

The soil in the South Carolina site where poison-ivy and poison-oak both occur lies between a sandy clay and loamy coarse sand and has been determined to be a sandy loam. The lower (poison-ivy) end of the gradient has finer textured soil than the upper (poison-oak) end and a higher Ca content than either the middle or upper end (44 ppm vs. 21 ppm in the middle vs. 16 ppm in the top for the A_1). The pH is slightly higher in the middle of the gradient than at either end. As the finer particles become less prevalent, the soil becomes more conducive to the growth of poison-oak and less to that of poison-ivy. The same is true as the calcium content drops, especially in the root zone of the A and upper B horizons (see Tables 24 and 25, and Fig. 62).

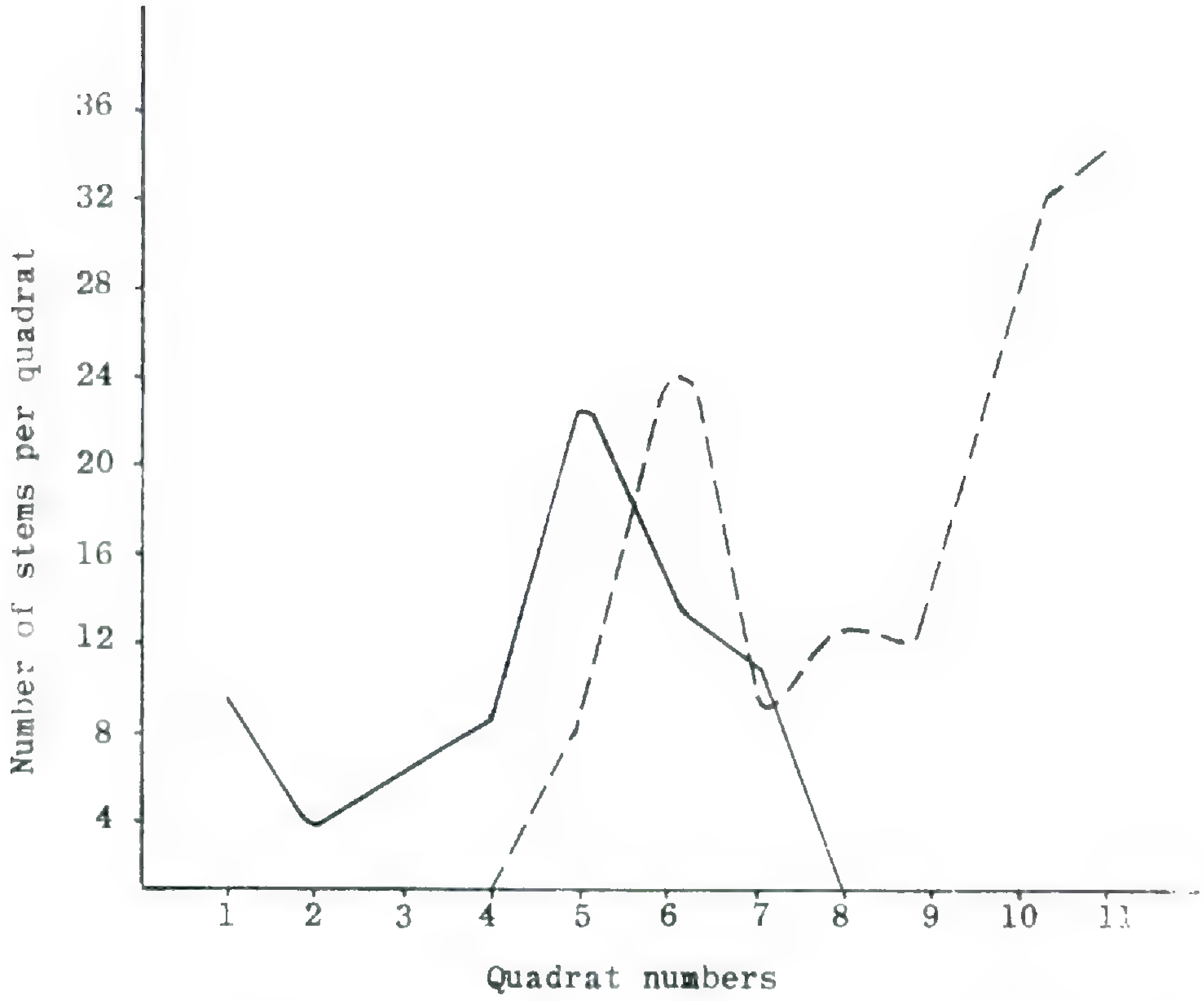
The Florida site is mapped in the Lakeland series (being only a few miles from the type location where the series was established) as a sandy loam. The texture is finer than that of the adjacent woods where only poison-oak grows, the soil of which is mapped as a Lakeland sand. The pH in the transition zone is higher and has a higher Ca content in the upper soil horizons than in the Lakeland sand which supports poison-oak but no poison-ivy.

The Mississippi site was determined to be on a Bude silt loam, poorly drained, low in fertility, and slightly eroded (Milbrandt, *et al.*, 1963). Its Ca content was moderate — 273 ppm — at the lower end of the presumed tolerance range for *Toxicodendron radicans* subsp. *radicans*, but higher than that recorded for most poison-oak sites. This soil may be looked upon as an intermediate habitat between the usual soil types in which either poison-ivy or poison-oak are normally found, but within the tolerance ranges of both. Although poison-ivy will usually live in the range of particle

DISTRIBUTION OF POISON-IVY AND POISON-OAK
ACROSS A SOIL TEXTURE GRADIENT

Richland Co., South Carolina, north of Columbia
Loblolly pine woods, 13 May 1961

Shrub quadrat data



Sandy clay sandy loam loamy coarse sand

———— Poison-ivy — — — — Poison-oak

Fig. 62. Distribution of Poison-ivy (*Toxicodendron radicans* subsp. *radicans*) and Eastern Poison-oak (*T. toxicarium*) across a soil texture gradient. Quadrat numbers are the average of two sub-quadrats each, measured along a line 110 m. long and sampled at 10 m. intervals.

size included in a silt loam, the low fertility of this profile makes it a marginal site for poison-ivy.

In summary, one may conclude that *Toxicodendron radicans* subsp. *radicans* inhabits soils which are higher in pH,

TABLE 24. SOIL PROFILE ANALYSIS OF OAK-PINE WOODS, COLUMBIA, SOUTH CAROLINA

Zone	Taxon	Gillis Collection Number	Horizon	Horizon Texture	pH	Ca	Mg	P	K
1	*T. radicans*	*4016*	A_1	sandy clay	4.47	44.5	8	2.4	8
			A_2	sandy clay	5.09	113.5	6	1	5.6
			B_1	sandy clay	4.68	37	5	1.6	6.4
			band in B_1	sandy clay	4.86	63	4	0.5	4.5
			B_2	loamy sand	4.73	15	0	1.0	4
			C	sand	4.38	113	20	1.1	12.4
2	*T. radicans*	*4569*							
	T. toxicarium	*4017*	A_0	sandy loam	5.82	11	0	1.1	3
			A_1	sandy loam	4.83	21	4	1.6	3
			A_2	sandy loam	5.52	15	8	1.5	8.5
			B_1	sandy loam	5.14	15	4	0.9	6
			B_2	sandy loam	5.57	10	6	9.6	2
			C	sand	6.51	85	12	15.8	12.5
3	*T. toxicarium*	*4600*	1	loamy sand	4.53	38	6	1.3	8.5
			2	loamy sand	4.33	16	2	1.7	2
			3	loamy sand	4.99	22	3	1.4	6
			4	sand	4.80	12	2	1.4	4.4

TABLE 25. SOIL PROFILE CHARACTERISTICS OF AREAS WHERE BOTH *T. RADICANS* AND *T. TOXICARIUM* GROW

Locality	Taxon	Gillis Collection Number	Soil Type	Horizon	Horizon Texture	pH	Ca	Mg	P	K
Mississippi	*T. radicans*	*5980*	Bude silt loam	A	loam	6.2	273	6.8	0.5	10.5
	T. toxicarium	*5979*								
S. Carolina	*T. radicans*	*4569*	Lakeland loamy sand	A_0	sandy loam	5.82	11	0	1.1	3
	T. toxicarium	*4017*		A_1	sandy loam	4.83	21	4	1.6	6.4
				A_2	sandy loam	5.52	15	8	1.5	8.5
				B_1	sandy loam	5.14	15	4	0.9	6

				B_2	sandy loam	5.57	10	6	9.6	2
				C	sand	6.51	85	12	15.8	12.5
Florida	*T. radicans* *T. toxicarium*	*4345*	Lakeland sandy loam	A_1	sandy loam	5.00	32	10	3	4.5
				A_2	sandy loam	5.25	28	12	2	4.5
				B	sandy loam	5.58	80	24	2.5	4.5
				C	sand	6.44	715	8	2	4.5

higher in nutrient concentrations (especially calcium and magnesium), and heavier textured than those in which *T. toxicarium* will grow. There is no clear-cut break between the requirements of one and the other, at least from the data presented herein, but rather an overlap of habitat requirements leading to the occasional ecotone wherein both species may be found intermixed. These ecotones are characterized by an intermediate type of soil, accompanied by an intermediate type of vegetation between a mesic woods and a sandhills vegetation — a woodland savanna.

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FAIRCHILD TROPICAL GARDEN
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GERMINATION AND DEVELOPMENTAL MORPHOLOGY OF SEEDS IN UTRICULARIA CORNUTA MICHX. AND UTRICULARIA JUNCEA VAHL[1]

Katsuhiko Kondo

An investigation of seedling morphology is often helpful in understanding the taxonomy of species but relatively few observations on seedlings of *Utricularia* have been reported (e.g., Goebel, 1891; Kumazawa, 1967). Morphology and physiology of seed germination and seedling growth of certain species of *Utricularia* in axenic cultures have been studied by Pringsheim (1962), Harder (1963), and Swamy and Mohan Ram (1969). All species used in their experiments were free floating or anchored aquatics; none was a terrestrial or epiphytic species. However, studies of the seedlings of terrestrial *Utricularia cornuta* Michx. and *U. juncea* Vahl are here reported for the first time.

Both *Utricularia cornuta* and *U. juncea* occur only in the New World. The former ranges from Texas to Florida, north to eastern Canada along the coast and westward to Upper Great Lakes, while *U. juncea* occurs in the eastern United States, West Indies, British Honduras, Trinidad, Guayana, Brazil, and perhaps Paraguay. In the southeastern United States, however, both taxa occur on the Coastal Plain.

Utricularia cornuta and *U. juncea* have sometimes been placed in the genus *Stomoisia* Raf. (Barnhart, 1913, 1915, 1933). Since both species are closely related, they needed to be examined for possible evidence which would contribute to a satisfactory taxonomic treatment, which stimulated me to make this study.

MATERIALS AND METHODS

Plants of *Utricularia cornuta* and *U. juncea* were col-

[1]This paper is a minor part of a thesis submitted to the Department of Botany of The University of North Carolina, Chapel Hill, in partial fulfillment of the requirement for the degree of Master of Arts.

Table 1. Field collections and their populations (the following list shows the field collections and their populations made in connection with this study).

Population No.		Collection No.	State & County	Locality
U-12	*U. cornuta*	534-536	North Carolina: Watauga Co.	Long Hope Creek Valley
U-22	*U. cornuta*	764-768	Florida: Nassau Co.	1 mile north of Hwy. U. S. 90, on Hwy. Fla. 121
U-2	*U. juncea*	970	North Carolina Duplin Co.	3.4 miles northwest of junction of Hwy. N. C. 50 & 53, on Hwy. N. C. 50, northwest of Maple Hill
U-3	*U. juncea*	968-969	North Carolina: Pender Co.	on dirt road which turns north of Hwy. N. C. 50, 2.2 miles southeast of Maple Hill
U-7	*U. juncea*		North Carolina: Brunswick Co.	3.3 miles north of junction 17 & 130, near Shallotte, on Hwy. N. C. 130
U-14	*U. juncea*	972	North Carolina: Brunswick Co.	4.1 miles northwest of Shallotte, on Hwy. N. C. 130

lected in North Carolina and Florida, from the populations listed in Table 1, and were brought to the greenhouse and grown under condition of high moisture and light intensity. Both species produced seeds which were used in this study. The following four media were used in the present study.

In the first medium, soil samples from the locality of the U-3 population were used. Two pieces of filter paper were put on soil samples in petri-dishes in which the pH was controlled by different mixtures of 0.2 M HCl and 0.5 M

NaOH. Four different solutions were used: a. pH 7.2; b. pH 4.5; c. pH 4.7; d. pH 5.1. Seeds of *Utricularia juncea* (U-3) were planted on the filter paper and kept in petri-dishes at room temperature (ca. 25°C).

In the second medium, a buffer solution was used. A stock solution was prepared by the following method: 4.88 gm of MES (2 N-Morpholino ethane sulfonic acid) in 250 ml. of distilled water was used to prepare 0.1 M buffer solution. This solution was diluted by adding 9 parts distilled water to 1 part stock solution. The pH of the buffer solution was adjusted with acid (0.2 M HCl) or base (0.5 M NaOH). Seeds of *Utricularia cornuta* and *U. juncea* were planted on filter paper with the buffer solution in the petri-dishes kept at room temperature.

The third medium was a solution of 500 ppm potassium gibberellic acid. Seeds of *Utricularia cornuta* (U-12 and U-22) and *U. juncea* (U-14) were planted on filter paper with this solution in petri-dishes kept at room temperature.

Moore's solution (Koch, 1967, pp. 14-15) was the fourth medium used. The fruits of *Utricularia cornuta* (U-12) and *U. juncea* (U-14) were first washed and sterilized with 100% ethylalcohol. Seeds were scooped from the sterilized fruits and spread in the medium in sterilized flasks.

RESULTS AND DISCUSSIONS

The results are listed on Table 2. The seeds of *Utricularia juncea* planted in a soil sample of pH 7.2, have not germinated. On many kinds of soil samples, however, the seeds have shown a low percentage of germination. Seeds of both species showed higher rate of germination only in Moore's solution.

Seedlings of the two species differ morphologically. Those of *Utricularia juncea* usually have only one chlorophyllose cotyledon and a second cotyledon, or a cotyledon-like structure, which lacks chlorophyll. The second cotyledon grows and develops into a rhizome on which some bladders and trichomes may be formed (Fig. 1-8, and 1-9). This seedling morphology is very similar to that observed by Goebel (1891) in the Asiatic *U. orbiculata* Wall., which was placed

Table 2. Germination data for planting at room temperature (ca. 25°C) of *Utricularia* seeds.

Species	Seed Identification Number	Medium	pH	Germination Percentages	No. of Seeds Used
U. cornuta	U-12-6	Buffer Solution	5.0	3.1	387
	U-22	Buffer Solution	5.0	2.9	724
	U-12-1	Gibberellic Acid	4.5	11.0	740
	U-22	Gibberellic Acid	4.5	10.8	259
	U-12	Moore's Solution	4.5 -5.0	87.4	144
U. juncea	U-3-1	Soil Sample	7.2	0.0	1310
	U-3-1	Soil Sample	4.5	7.0	935
	U-3-1	Soil Sample	4.7	2.5	1225
	U-3-1	Soil Sample	5.1	1.5	1531
	U-2-2	Soil Sample	5.1	1.0	1260
	U-7-1	Buffer Solution	4.5	13.4	156
	U-14	Gibberellic Acid	4.5	8.2	415
	U-14	Moore's Solution	4.5 -5.0	98.3	3650

in *U. striatula* Sm. by Taylor (1964). The most interesting observation was that *U. cornuta* showed two types of seedling morphology, correlated with different media. In buffer or Moore's solutions, the seedlings were similar to those of *U. juncea* in that one green cotyledon and one cotyledon-like structure, which developed into a rhizome, were formed. However, the angle between these structures was quite different from that in seedlings of *U. juncea* growing in buffer or Moore's solution. The other type of *U. cornuta* seedling was the normal two-cotyledon type which developed in gibberellic acid solution (Fig. 1-1 to 1-7). This type of germination is that usually shown in aquatic species of *Utricularia*

Fig. 1. Seedlings of: — 1-7. *Utricularia cornuta*; — 8-9. *Utricularia juncea*. 1-2. Germination; 3. Seedling with one cotyledon (Ct) with chlorophyll and cotyledon-like structure (Cl) which lacks chlorophyll; 4. Seedling with a cotyledon-like structure developing into the rhizome (Rz); 5. Seedling with two normal cotyledons (Ct); 6. Seedling with two cotyledons (Ct) and the first leaf (Lf); 7. Seedling with two cotyledons, the first leaf, and the second leaf growing; 8-9. Seedling with one cotyledon and a cotyledon-like structure developing into the rhizome with some trichomes.

(e.g., Kumazawa, 1967). Collections of seeds from two geographically diverse populations, U-12 from Watauga Co., North Carolina and U-22 from Nassau Co., Florida, gave the same results. This might be a mechanism for adaptation to some unknown environmental factor to which populations are exposed.

ACKNOWLEDGMENTS

I wish to express sincere appreciation to Dr. C. R. Bell, Department of Botany, The University of North Carolina, who directed my research program and has been especially helpful in many other ways. I am similarly indebted to Dr. A. E. Radford and Dr. C. R. Parks, Department of Botany, The University of North Carolina, for their interest and helpful suggestions during the preparation of this thesis. Appreciation is also expressed to Dr. N. G. Miller, Department of Botany, The University of North Carolina, and Dr. A. J. Sharp, Department of Botany, The University of Tennessee, for their interest in this work and for reading the manuscript.

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ATRIPLEX PATULA VAR. HASTATA SEED DIMORPHISM

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Seeds were collected from a population of *Atriplex patula* var. *hastata* (L.) Gray on October 3, 1964 from saline marshes surrounding Lincoln, Nebraska (Ungar, Hogan, and McCelland, 1969). The seeds contained in bracteoles were dimorphic, both light and dark colored forms being found. The dark colored seeds had a hard black testa while the light colored seeds appeared naked and yellowish-brown. A check of taxonomic manuals, Gleason (1952), Fernald (1950), Gleason and Cronquist (1963), Rydberg (1932), and Mason (1957) does not indicate any seed dimorphism in *A. patula* var. *hastata*. Beadle (1952), in an ecological study of several Australian *Atriplex* species, found that two, *A. inflata* and *A. semibaccata*, produced both soft and hard seeds. In a study of several other *Atriplex* species introduced to Canada, Frankton and Bassett (1968) illustrate for *A. patula* var. *hastata* what appears to be a large naked seed and a smaller seed containing a hard seedcoat, with the larger seed possessing a larger bracteole than the smaller. The introduced species described by Frankton and Bassett, *A. heterosperma* Bunge, *A. oblongfolia* Waldst. et Kit., and *A. hortensis* L. were dimorphic in seed form, having a larger yellowish-brown seed, 2-4 mm in diameter, depending upon the species, or a smaller seed, 1-2 mm in diameter, with a hard black testa. Quantitative data concerning seed form and germinability is provided in this present study for *A. patula* var. *hastata* which occurs in North America.

Measurements were made with a binocular microscope, containing an ocular micrometer, of 100 seeds of each morphological type. The soft, yellowish-brown seeds range from 1.4 to 2.5 mm in diameter and have a mean diameter

[1]This research was supported by National Science Foundation research grant GB6009.

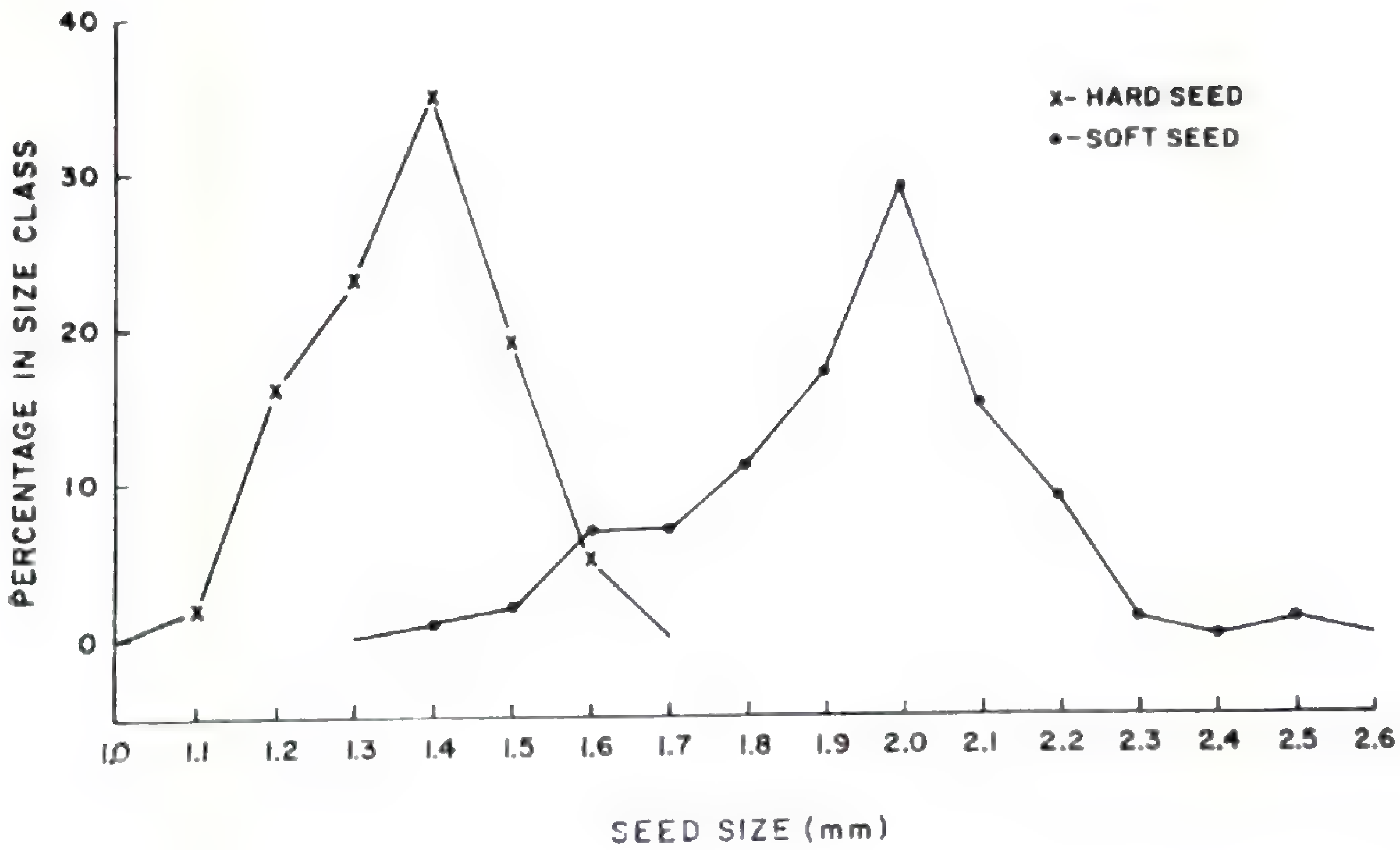

Figure 1. Seed size dimorphism in *Atriplex patula* var. *hastata.*

of 2.0 mm. Hard, black seeds range from 1.1 to 1.6 mm in diameter and their mean diameter equals 1.4 mm. A t test analysis indicates that differences in seed diameter are significant at $P \leqq 0.01$ (Figure 1). Measurements of bracteoles indicate that black seeds can be found in those ranging from 1.0 to 4.0 mm in length and yellowish-brown seeds in bracteoles ranging from 2.6 to 5.0 mm in length.

Preliminary seed germination studies, using 100 seeds of each type, in December, 1967 on three year old seed indicated that only yellowish-brown seed germinated while the black seed had a dormancy. It was found that scarification of the black seed-coat would break this dormancy. Germination percentages for yellowish-brown seed averaged 43% at this time. A study of six year old seed in December, 1970, using 100 seeds of each type gave different results. Four groups of 100 seed were germinated, scarified and unscarified, yellowish-brown and black. Black unscarified seed had 0.0% germination, while the black scarified seed appeared to have retained a high viability, 73% germination (Table 1). The yellowish-brown seed did not retain their high viability, 43%, over the six year refrigerated storage

period, having only a 6% germination over the 20 day germination period. These data are in agreement with the results of Beadle (1952) for Australian *Atriplex* species.

Table 1. Germination percentages of dimorphic seed after six years of dry refrigerated storage.

Days	5	10	15	20
% Soft Seed	5	5	6	6
% Unscarified Hard Seed	0	0	0	0
% Scarified Hard Seed	46	68	72	73

Seed dimorphism may play a very significant role in determining survival of halophytic annual species such as *A. patula* var. *hastata*. In areas of low rainfall seedlings developing from soft seeds may perish due to inadequate moisture, while hard seeds which do not germinate immediately are less liable to die. A low rainfall period may be enough to support germination but inadequate for completion of growth. Seeds with soft testa will germinate and have no initial dormancy, although the hard, black seeds will germinate only after the testa is scarified. The black seeds are therefore more resistant to short term environmental hazards. As indicated by these laboratory studies black seeds retain their ability to germinate for longer periods and therefore can be stored in the soil for longer periods. Since *A. patula* var. *hastata* occurs in saline soils, a dormancy allows seeds to overcome periods of high salinity stress and resume germination when the soil moisture stress is reduced. Beadle (1952) reports 0% germination of light colored seeds of *A. inflata* and 28% for dark seed after a six year storage period, while freshly collected seed had 100% germination. Another Australian species, *A. vesicaria*, had 92% initial germination of light seed while after six years only 44% germinated. These results are similar to the data found for *A. patula* var. *hastata* which had 73% germination for scarified black seed and 6% germination for unscarified and 29.0% for scarified light seed after six years. Evidently the larger, soft, yellowish-brown seed be-

come more dormant in storage while the hard black seeds retain the ability to germinate for long periods. Seed dimorphism probably has survival value in extreme environments and in the evolution of seed in *Atriplex* species both a rapidly germinating and a dormant form of seed have developed.

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NEW TAXA, COMBINATIONS AND DISTRIBUTION RECORDS FOR THE OKLAHOMA FLORA

U. T. WATERFALL*

Progress on a Concise Flora of Oklahoma makes it desirable to publish the following items. Specimens cited are deposited in the Herbarium of Oklahoma State University (OKLA) unless otherwise stated.

Rhynchospora caduca Ell. was collected as *Steve Stephens* 27696 (KANU) from moist rocky soil, wooded bank of small creek, 10 miles north of Broken Bow, McCurtain County, Aug. 17, 1968. It has been known previously from as far west as Benton County, Arkansas, and extreme eastern Texas (Gale, 1946).

Juncus crassifolius Buchenau, Monog. Junc. 326, 1890, should be used for the representatives of the taxon passing as *J. validus* Coville, Bull. Torr. Bot. Club 22: 305, 1895. Coville rejected Buchenau's name, offering his own epithet as a nom. nov., because there existed a name, belonging to another taxon, *J. polycephalus* Michx., var. *crassifolius* Michx., Fl. Bor. Amer. 1: 192, 1803. This procedure may have represented the correct application of The American Code of Botanical Nomenclature, under which Coville was working, but according to the International Rules a name carries priority only in its own rank. Therefore Buchenau's epithet is available and Coville's is superfluous.

We have var. *crassifolius* in the eastern half of Oklahoma. The endemic Texas variety, occurring north and south across central Texas, becomes **Juncus crassifolius** Buch. var. **fascinatus** (M. C. Johnston) Waterfall, comb. nov. based on *J. validus* Cov. var. *fascinatus* M. C. Johnston, Southw. Nat. 9: 313, 1964.

Tipularia discolor (Pursh) Nutt. was collected by *Steve Stephens* 27718 (KANU) pine-deciduous forest hillside, 2

*Dr. Waterfall died in October, 1971.

miles south of Honobia, LeFlore County, Aug. 18, 1968. It was previously known as far west as Garland and Hempstead counties, Arkansas, and Hardin and Jasper counties, Texas (Correll, 1950).

Atriplex patula L., var. **hastata** (L.) Gray. So referred is *Waterfall* 10397, sand, dried bed of Cimarron River, south of Waynoka, Woods County, Oct. 6, 1951. Most of the leaves have fallen from the specimen, but the separate pistillate bracts, some of which are more or less hastate, would seem to positively place it as a representative of this taxon.

Argemone polyanthemos (Fedde) G. B. Ownb., forma **rosea** Waterfall, f. nov., petalis roseis. The petals are pink and the filaments are suffused with pink. In forma *polyanthemos* the petals are white and the filaments are yellow. HOLOTYPE: *Waterfall* 13147 (OKLA), sand, 10 miles south and 3 miles west of Stillwater, Payne County, June 10, 1957.

Hypericum hypericoides (L.) Crantz, var. **multicaule** (Michx.) Waterfall, comb. nov., based on *Ascyrum multicaule* Michx., Fl. Bor. Am. 2: 77. 1803. *Ascyrum hypericoides* L., var. *multicaule* (Michx.) Fern.; *Hypericum stragalum* Adams & Robson, Rhod. 63: 15. 1961. This taxon seems no more than varietally distinct from *H. hypericoides* var. *hypericoides*.

Viola pubescens Ait., var. **eriocarpa** Nutt., Genera of N. Amer. Plants 1: 150, 1818, not var. *eriocarpa* (Schwein.) Russell, based on *V. eriocarpa* Schwein., 1825, should be used as the name of the hairy-fruited taxon of *V. pubescens* Ait. Nuttall (l.c.) stated "*β eriocarpon.* Fruit densely villous . . . In fruit this would be taken for a distinct species . . . in any other respect it does not materially differ from *V. pubescens*; both these varieties are abundant near Philadelphia."

Argythamnia humilis (Engelm. & Gray) Muell. Arg., var. **leiosperma** Waterfall, var. nov. seminibus laevibus vel sublaevibus. Toward the western part of its range in Oklahoma is a population which has smooth seeds, contrasting

with var. *humilis* which has seeds marked with rugose-roughened areas. HOLOTYPE: *Waterfall* 9735 (OKLA) top of Black Mesa, 3 miles north of Kenton, Cimarron Co., Oklahoma, Oct. 7, 1950. Other collections: **Oklahoma**, CIMARRON COUNTY: *Waterfall* 7893 arroyo up north slopes of Black Mesa, 3 miles north and 1 west of Kenton, June 13, 1948; *Waterfall* 8647, along an arroyo running up the north slopes of Black Mesa, 2.5 miles north and 1 west of Kenton, Aug. 23, 1948; *Waterfall* 9231, top of Black Mesa, 3 miles north and 1 west of Kenton, Aug. 9, 1949. **Texas**, BROWN COUNTY: *Stanford* 825, disturbed grassland, 3 miles south of Brownwood, Apr. 15, 1967; *Stanford* 1180, banks of Adams Branch Creek, 2 miles west of Brownwood, May 30, 1967. HAMILTON COUNTY: *Stanford* 1477, prairie, dark limestone soil, 3 miles northwest of Aleman, Sept. 4, 1967; *Stanford* 1482, prairie, 4 miles south of Aleman, Sept. 4, 1967.

Convolvulus incanus Vahl, forma **roseus** Waterfall, f. nov., corollis roseis. The entire corolla is pink. This forma appears to be more abundant westward. HOLOTYPE: *Waterfall* 14895 (OKLA), valley north of Black Mesa, north of Kenton, Cimarron County, Oklahoma, June 7, 1958.

Gaillardia lanceolata Michx., var. **flavovirens** Mohr, Contr. U. S. Natl. Herb. **6**: 812, 1901; *G. lutea* Greene, Pittonia **5**: 57, 1902; *G. chrysantha* Small, Fl. SE. U. S., 1293, 1903; *G. serotinum* (Walt.) H. Rock, Rhodora **58**: 315, 1956. This phase with yellow disc corollas, of sporadic occurrence, hardly seems separable as a species. We have it from Cherokee, Muskogee and Payne counties. Although the type of var. *flavovirens*, from Baldwin County, Alabama, is said to be rayless our material has ray corollas.

The variety of local occurrence in Hardin County, Texas becomes **Gaillardia lanceolata** Michx., var. **Winkleri** (Cory) Waterfall, comb. nov. based on *G. lutea* Greene, var. *Winkleri* Cory, Madrono **8**: 263-264, 1946.

Helianthus silphioides Nutt. was collected by *Steve Stephens* 27763 (KANU), moist sandy soil on steep wooded

hillside, 1.5 miles northwest of Honobia, Pushmataha County, Aug. 18, 1968. We have specimens from the eastwardly adjacent state of Arkansas.

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CHROMOSOME NUMBER OF LYSIMACHIA CILIATA L.

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Cytological investigations are important to clarify the nature and extent of the internal chromosomal diversity in the species of *Lysimachia*.

Lysimachia ciliata (Primulaceae) is commonly found in open swamps, marshes, stream banks and ranges from Newfoundland to British Columbia. The material in the vegetative stage from Quetico Park was received from Dr. N. K. McEwen under the name of *Prunella vulgaris*. Chromosome number of $2n = 96$ (Fig. 1) was determined from root tips by pretreating the roots with paradichlorobenzene for three hours, hydrolyzing them in N.HCl for about ten minutes at 60°C., and subsequently squashing them in 2% acetocar-

Fig. 1. Chromosomes in root tip cell of *Lysimachia ciliata* L. $2n = 96$.

mine. For meiotic investigations, material from Alterive lake, Galt, Ontario (CAN L. S. GILL 296) was fixed in acetic alcohol and chromosome counts were made by the acetocarmine squash method. The meiotic divisions in the PMC's were regular and 48 bivalents were observed at M-I in temporary preparation.

The present counts of $2n = 96$ do not agree with the previous count of $2n = c72$ (Smith 1964c). Base numbers are 9, 12 and 14 (Darlington & Wylie 1955) and *L. ciliata* is octaploid with $x = 12$. However, the reports of $2n = 16$ in *L. nemorum* and $2n = 32$ in *L. nummularia* (Gadella & Kliphuis 1963), $2n = 30$ in *L. punctata* (Reese, 1953 and Taylor and Mulligan, 1968), $2n = 20$ in *L. japonica* (Borgman, 1964) and in *L. mauritiana* (Chuang, *et al.*, 1963), are indicative of new base numbers of 8, 10 and 15, for this genus. Thus the genus *Lysimachia* shows heteroploidy and its basic chromosome numbers are 8, 9, 10, 12, 14 and 15. About 55.17% of the species of this genus investigated to date are polyploids.

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ON THE NOMENCLATURE OF SALIX BEBBIANA SARG.

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Youngberg has recently proposed to treat *Salix bebbiana* Sarg. as a subspecies of the Eurasian *S. starkeana* Willd., under the name *S. starkeana* subsp. *bebbiana* (Sarg.) Youngberg, Rhodora 72: 549. 1970. This name is illegitimate and must be rejected under the International Code of Botanical Nomenclature.

As Youngberg notes, the name *S. bebbiana* Sarg. was based on *S. rostrata* Richardson, App. Frankl. Journ. 753. 1823, a later homonym of *S. rostrata* Thuill. 1799. Some other nomenclatural synonyms of *S. rostrata* Richardson which need consideration here are:

S. vagans subsp. *rostrata* Anderss. Svenska Vet.-Akad. Handl. **6**: 87. 1867.

S. depressa subsp. *rostrata* Hiitonen, Memoranda Soc. Fauna Fl. Fenn. **25**: 82. 1950.

The Andersson name was published as a binomial subspecies, a form which would seem on its face to be illegitimate, but which is effectively legitimized by a statement in the examples under Article 24 of the current (1966) edition of the International Code of Botanical Nomenclature. Article 60 of the Code provides that "When the rank of a genus or infrageneric taxon is changed, the correct name or epithet is the earliest legitimate one available in the new rank. In no case does a name or epithet have priority outside its own rank." Article 66 further provides that "An epithet originally published as part of an illegitimate name may be adopted later for the same taxon in another combination", and this provision is elaborated on in Article 72. Thus the fact that Richardson's name *S. rostrata* is illegitimate has no bearing on the choice of a subspecific epithet. In subspecific rank the epithet *rostrata* carries priority from 1867. Hiitonen himself pointed out that he adopted the subspecific epithet *rostrata* because its prior use by Andersson

foreclosed the possibility of using the epithet *bebbiana* in that rank.

It is therefore clear that Youngberg's name falls afoul of Article 60 (previously quoted) and of Article 67, which states "A specific or infra-specific epithet is illegitimate and must be rejected . . . if its author did not adopt the earliest legitimate epithet available for the taxon with its particular circumscription, position, and rank". We may note again that the several names here discussed, aside from *S. rostrata* Thuill., are all nomenclatural synonyms, with *S. rostrata* Richardson as the basionym.

If the plant now generally known as *Salix bebbiana* Sarg. is to be treated as a subspecies of *S. starkeana*, it must take the subspecific epithet *rostrata.* I deliberately avoid the formal new combination, and I express no opinion here as to the proper taxonomic status of the group.

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THE REEVALUATION OF THE GENUS CLIOCOCCA (LINACEAE) OF SOUTH AMERICA

C. M. Rogers and R. Mildner

During the course of preparing a revision of *Linum* in South America, it has become necessary to review the position of the aberrant species *L. selaginoides* Lam. in the genus. It is very different from other South American species; study of the North American flaxes (Rogers 1963, 1968) and examination of the Old World species at Kew (K), Paris (P) and Geneva (G) reveal that it is equally distinct from other species of the genus (Fig. 1).

Few of these differences are revealed in Lamarck's original description of the species as *L. selaginoides* (1791). Babington (1842), however, noted several of its peculiarities when he established the genus *Cliococca* for it. The material upon which he based his description came from plants grown in the Cambridge Botanical Garden from seed he thought had been collected in New South Wales by a "Mr. Melluish, whilst accompanying a party in pursuit of bushmen." There are no plants resembling this species from that region, and it is clear from both his text and accompanying illustrations that it was the South American plant that he had before him.

Planchon (1848) retained the species in the genus *Linum*, establishing the subgenus *Cliococca* for it, a disposition which has been continued since.

The authors have now had the opportunity to examine about two hundred collections of this species, to observe it in the field and to grow plants to maturity in the greenhouse. It is evident that it differs from *Linum* in a number of important characteristics and that it is probably only distantly related to any species of that genus. Although *Linum*, a genus of about 150 species, shows a substantial amount of variation, there are numerous intermediates which tend to tie the species into a clearly related whole. This is not

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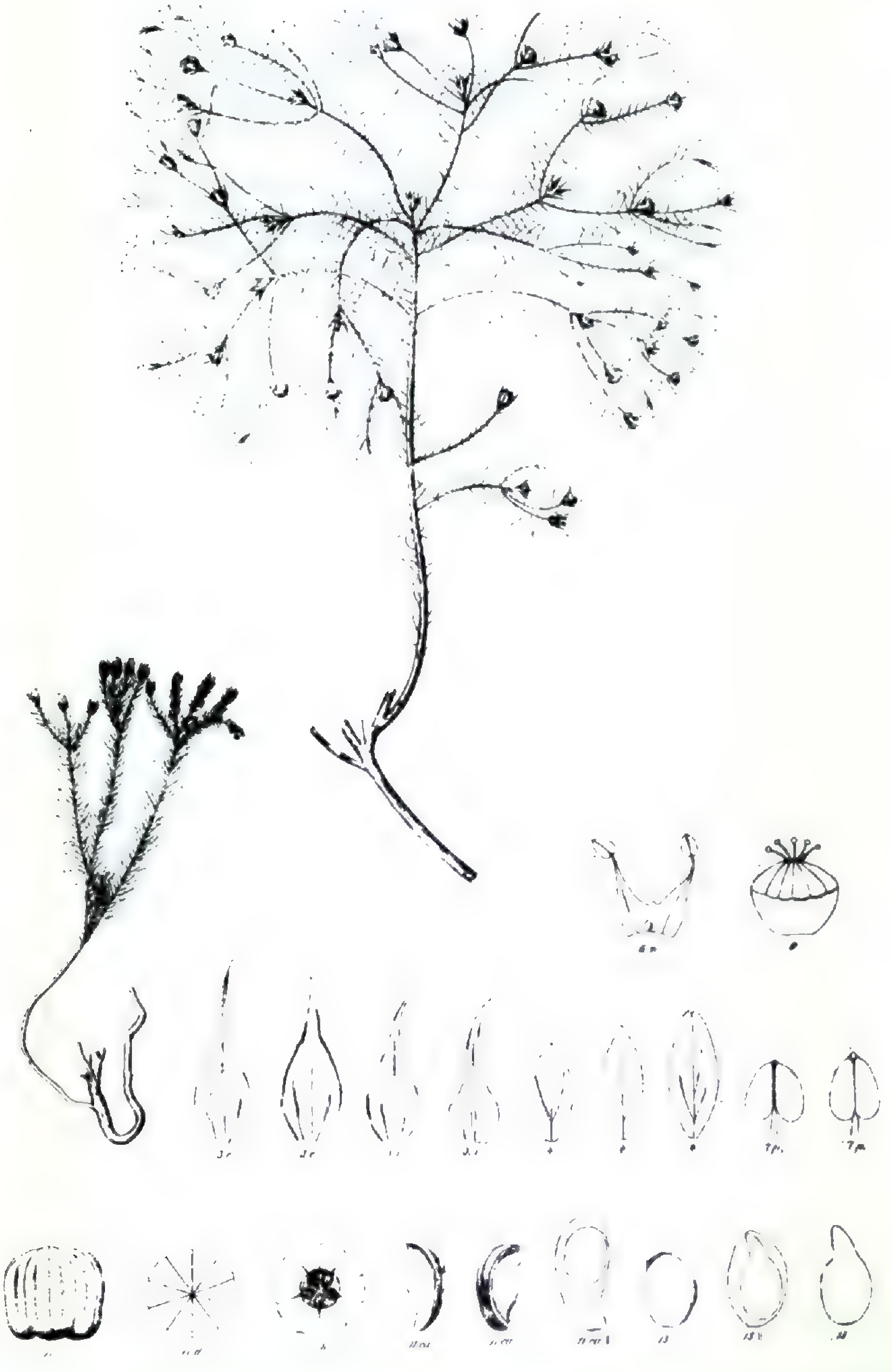

LINUM selaginoides.

Figure 1. Habit and floral parts of *Cliococca selaginoides.* From Urban in Martius' Flora Brasiliensis.

the case with *L. selaginoides*, which stands well apart. Its segregation into another genus properly reflects this and it is therefore proposed to resurrect the genus *Cliococca*. In the following description, the features which generally distinguish it from *Linum* are italicized. Some of these are amplified in the discussion which follows.

Cliococca Babington, Trans. of the Linn. Soc. of Lond. **19**: 33. 1842. Perennial, glabrous herb, 9-25 (5-38) cm tall, simple or branched at the base and in the inflorescence, the often decumbent, *very leafy stems arising from an extensive, branched, underground rootstock;* leaves alternate, imbricate, 1-nerved, linear, the larger 6.0-9.6 (5-11) mm long, 0.4-0.6 (0.2-0.7) mm wide, spreading; stipular glands none; *flowers few, terminal on stems or branches*; sepals five, lanceolate, 3 to 5-nerved, margins entire, the outer larger, these 4.8-5.4 (4-6) mm long; petals five, *imbricate*, oblanceolate with a short claw, *whitish or tinged with pale pink*, 2.3-3.2 mm long, *shorter than the sepals*; stamens five, ca 2 mm long, united at the base, with small, deltoid intervening staminodia or these sometimes absent; anthers ovate-cordate, ca 0.5 mm long; styles five, separate, *ca 0.4-0.9 mm long*; stigmas capitate; fruits broadly obovate, flattened at the summit, 2.9-3.5 (2.5-3.7) mm high, 3.2-3.7 (2.9-3.9) mm in diameter, outer walls thick; *false septa complete, the fruit ultimately separating into* 10 *indehiscent* 1-*seeded segments*; seeds light brown, elliptic, ca 1.7 mm long, 1.0 mm wide; pollen tricolpate; chromosome number, $n = 18$ (Darlington and Wylie, 1955).

Although there are sufficient resemblances between *Cliococca* and *Linum* that the latter must be considered the most closely related genus, it is not clear with what portion of *Linum* its affinities lie. The extensive underground rootstocks are apparently unknown in *Linum*. Except for a juvenile plant or two, none of the herbarium specimens of *Cliococca* examined had complete rootstocks, although some were several inches in length and possessed a number of aerial stems. It is likely that colonies of considerable extent

may very well result from this kind of vegetative reproduction. Plants grown in the greenhouse seem to be facultative apomicts; if so, asexual reproduction may be accomplished by seeds as well. In nearly all species of *Linum* the inflorescence is a paniculate or racemose cyme; only *L. imbricatum* and *L. hudsonioides*, two North American species not very closely related to *Cliococca*, have inflorescences resembling it. The manner in which the false septa are completely developed, resulting in the fruit separating into ten indehiscent segments is unknown in *Linum*, except, possibly, in the otherwise very different African *L. keniense*. The very short styles and the petal color and size are different from species of *Linum*; corollas in *Linum* are uniformly convolvulate while in *Cliococca* they are imbricate. The pollen is also quite different. Xavier (1967) in a worldwide survey of the genus, divided the pollen of *Linum* into sixteen types. That of *L. selaginoides* constituted one type, and he stated that its unique pollen morphology would support placing the species in a separate genus. When these several characters are considered, it is clear that the plant is most properly removed from *Linum*.

There is but a single species, widespread and sometimes weedy, in a variety of habitats in south-central South America (Fig. 2).

Placing this species in the genus *Cliococca* requires the following new combination:

Cliococca selaginoides (Lam.) Rogers and Mildner, **comb. nov.** Type: Uruguay: Montevideo, *Commerson* (P!)

Linum selaginoides Lam. Encycl. 3: 525. 1791.

Cliococca tenuifolia Bab., Trans. Linn. Soc. Lond. 19: 34. Tab. III. 1842.

Linum babingtonii Planch., Lond. Jour. Bot. 7: 179. 1848. Based on *C. tenuifolia* Bab.

Linum selaginoides Lam. var. *chilense* Planch., Lond. Jour. Bot. 7: 179. 1848. Type: Chile: Valdivia, *Bridges* 669 (K!).

Linum mycrophyllium Larr., Escritos Larrañaga 2: 122. 1923. Based on *L. selaginoides* Lam.

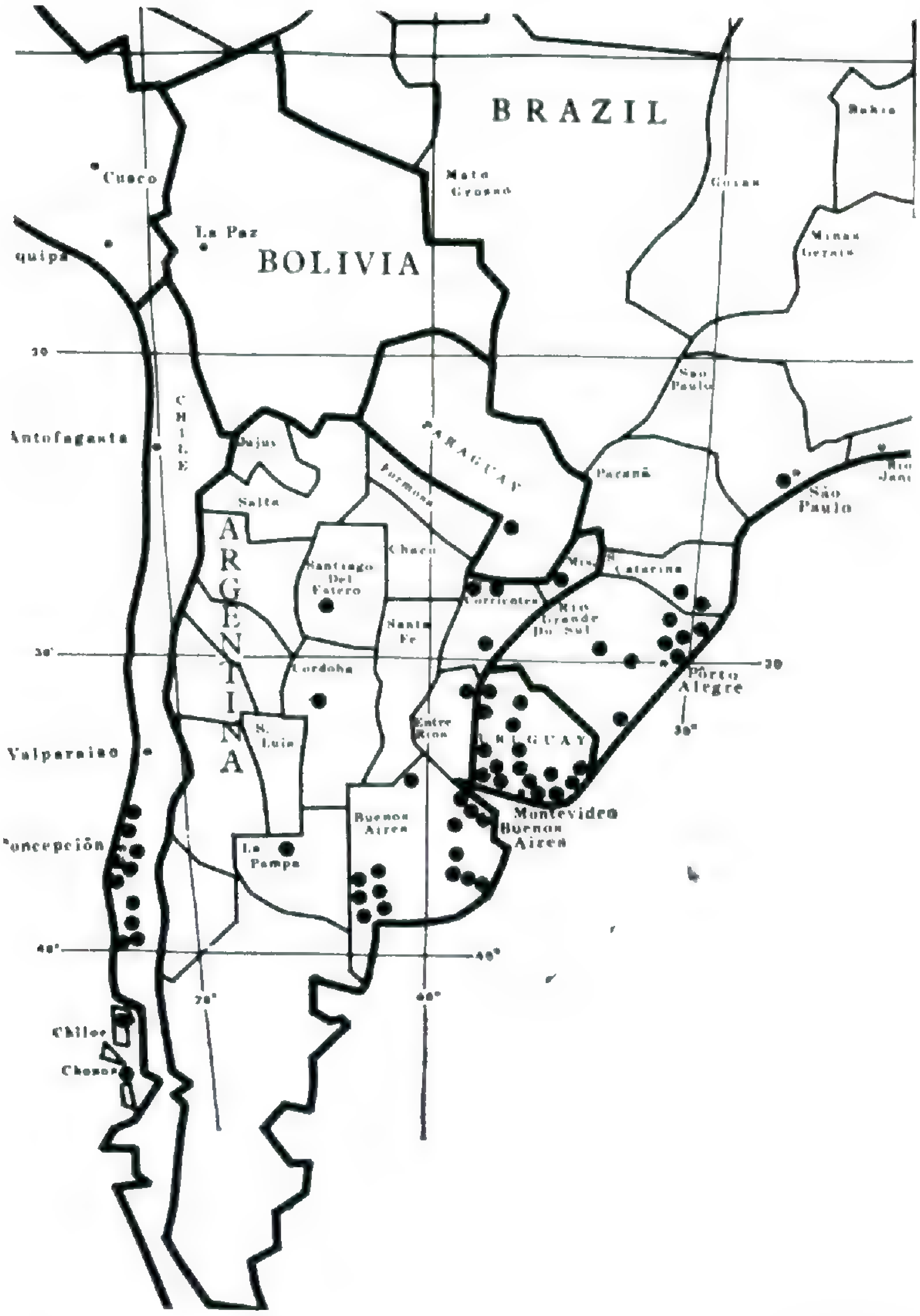

Figure 2. Distribution of *Cliococca selaginoides* in South America. The location in Paraguay is only approximate.

These studies were supported by a Sigma Xi Grant-in-Aid of Research.

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FLEISCHMANNIA AND CONOCLINIUM (COMPOSITAE, EUPATORIEAE) IN EASTERN NORTH AMERICA

JEAN W. WOOTEN AND ANDRÉ F. CLEWELL

King and Robinson (1970a-e) have fragmented the large and variable genus, *Eupatorium* L., placing the great majority of the species in a number of other genera. Grashoff and Turner (1970) contended that the segregate genera were poorly defended by King and Robinson and that the reliability of the microcharacters, which were liberally used in generic circumscription by King and Robinson, has yet to be determined. On the basis of gross morphology, chromosome number, and distribution, we feel that the removal of several North American species from *Eupatorium* into the segregate genera as proposed by King and Robinson will result in a more natural and less unwieldy classification. On the other hand, our knowledge is largely limited to the North American taxa. We realize that additional studies on the many neotropical species might precipitate further generic realignments.

The eastern North American species which are usually considered as members of *Eupatorium* have been assigned to five genera. King and Robinson (1970e) retained 21 species in *Eupatorium*; a few others omitted by King and Robinson, e.g., *E. compositifolium* Walt., should probably be added. The four verticillate-leaved species were transferred to *Eupatoriadelphus* (King and Robinson, 1970d). Three additional species, including the white snakeroot, are now placed in *Ageratina* (Clewell and Wooten, 1971). One species each has been placed in *Fleischmannia* and *Conoclinium* (King and Robinson, 1970a, c). These latter two species are the subject of the present paper.

Plants of both species were observed in natural populations in Leon County, Florida. Seeds from these populations germinated immediately without pretreatment and were grown in a greenhouse. Buds and root tips were also ob-

tained and fixed in Carnoy's fluid for cytological analysis, and were later squashed and stained with aceto-orcein. Dried specimens were examined from the following herbaria: FLAS, FSU, GA, GH, ILLS, IND, ISC, KSC, KY, LAF, MICH, MO, NEBC, NO, NY, OKL, OS, PAC, SMU, TENN, TEX, UMO, UNC, VDB, VPI, WVA, Georgia Southern College, and the University of Mississippi. Drawings of plants were made by Barbara N. Culbertson.

Fleischmannia incarnata (Walt.) R. M. King & H. Robinson, Phytologia **19:** 203. 1970.

Eupatorium incarnatum Walt., Fl. Car. 200. 1788.

Kyrstenia incarnata (Walt.) Greene, Leaflets Bot. Obs. Crit. **1:** 8. 1903.

Stems weak, often sprawling, puberulent, up to ca. 1.5 m long; leaves opposite, membranous, deltoid, usually narrowly so, the largest blades up to 2-8 cm long, sparsely to moderately pilose, sometimes glandular-punctate beneath, apices acute or nearly acuminate, bases truncate, sometimes subcordate or broadly cuneate, margins crenate or uncommonly nearly serrate, the teeth sometimes irregular in size and shape on the same leaf, the largest blades 1.5-3 times longer than their petioles; heads borne in moderately dense to loose corymbs, some of the terminal pedicels being at least 4 mm long and (in the Southwest) up to 25 mm long, each head bearing ca. 20-23 flowers; involucres comprised of 15-18 phyllaries, imbricated towards the base and arranged in 3 or 4 series: the outer 1 or 2 series comprised of usually 3-5, ovate-cuspidate or lanceolate, short phyllaries ca. 2 mm long (appearing similar to the 2 or 3 bracts closely subtending the involucre), the inner 2 series comprised of 12 or 13 phyllaries, (3-)4-5 mm long, subequal, linear-acuminate or acute and 2-nerved or narrowly oblong-mucronate (uncommonly obtuse) and weakly nerved, sparsely pubescent; corollas 2-3 mm long, tubular, constricted at the base at anthesis, the lobes mostly 1/4-1/6 as long as the tube, lavender, glabrous, sometimes finely glandular-punctate beneath (best seen in bud), the tube white, often with purple

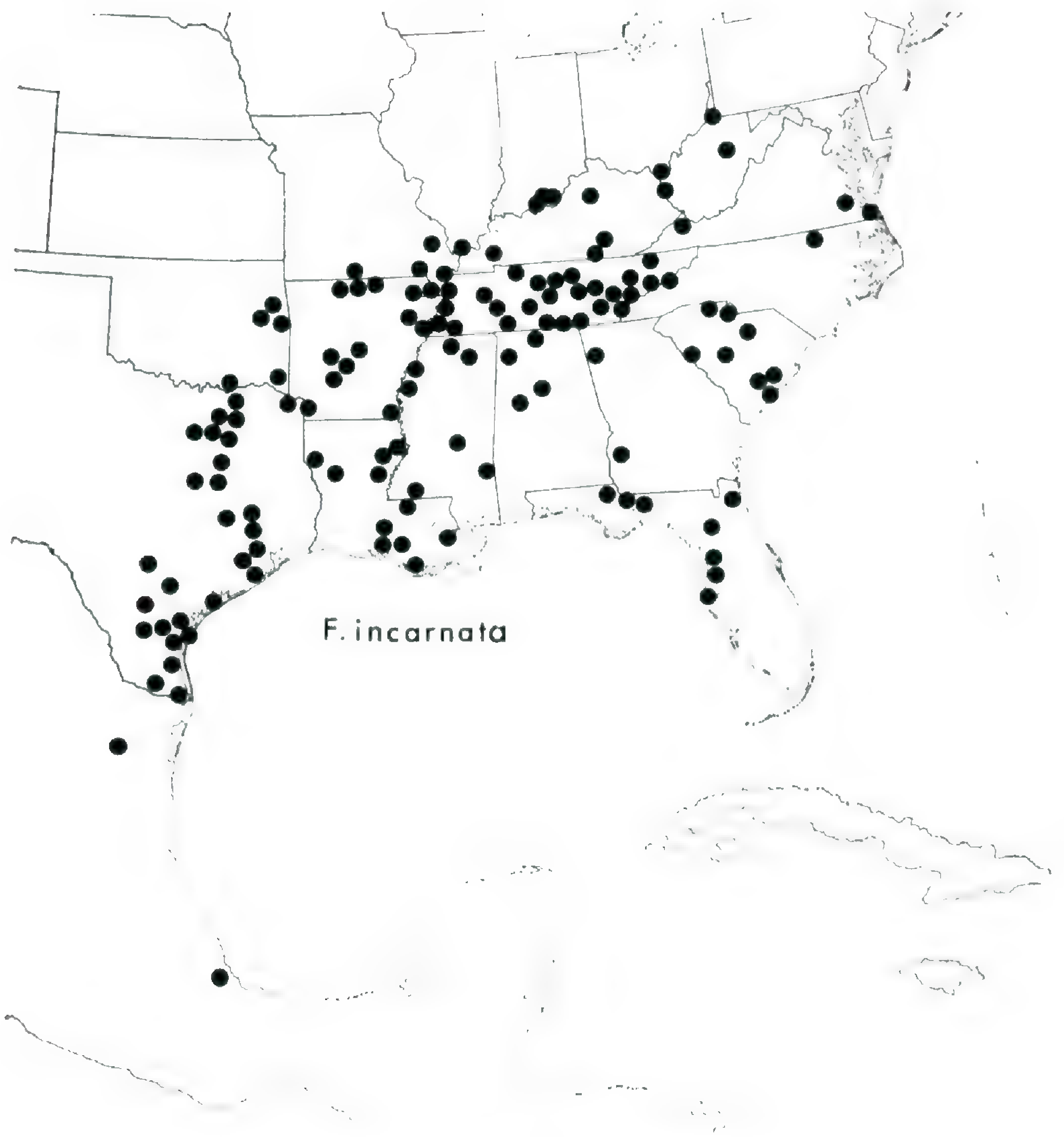
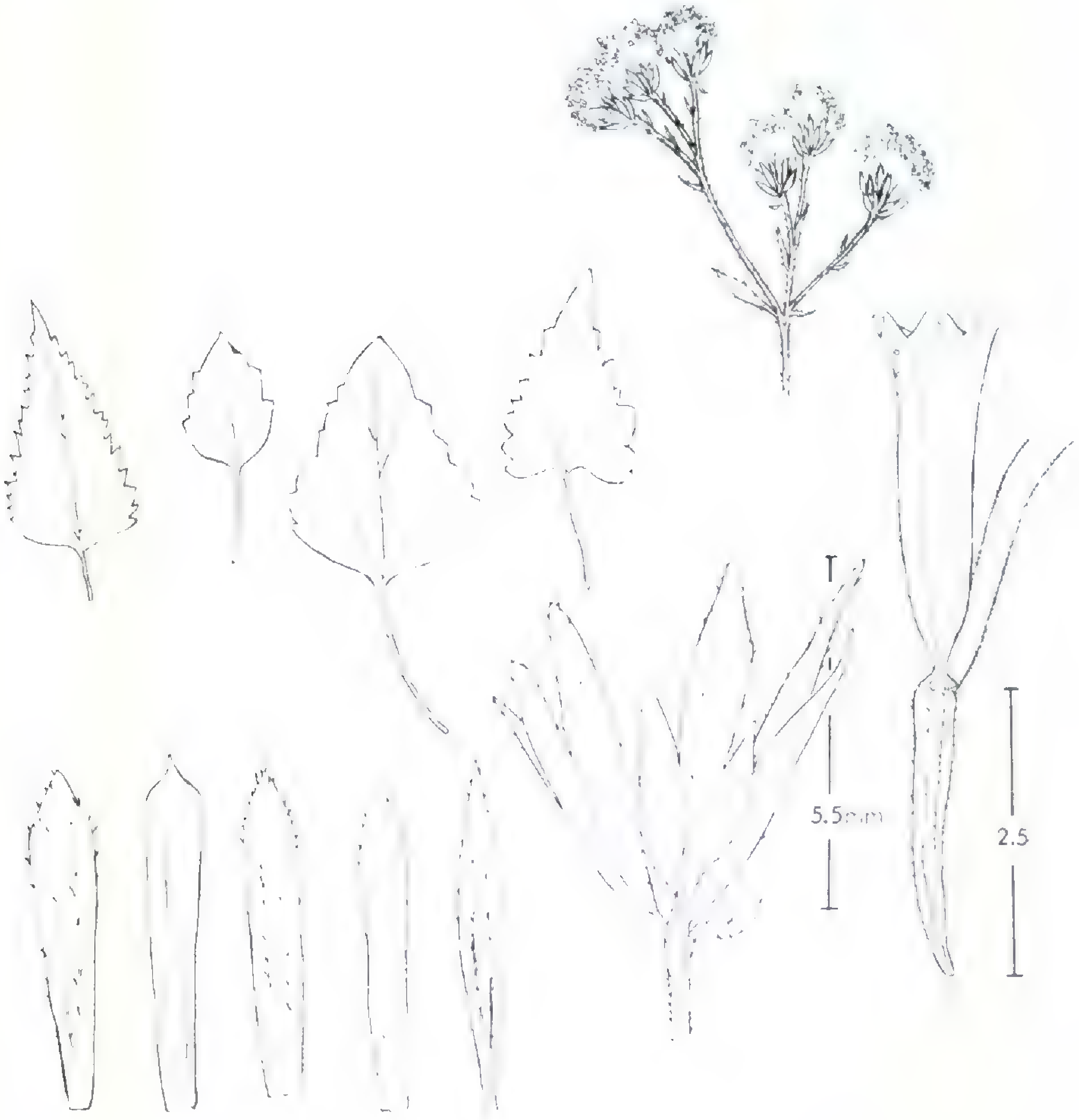


Figure 1. Distribution by county of *Fleischmannia incarnata.*

Figure 2. *Fleischmannia incarnata* (above), including a fertile branch, an involucre, four leaves, five phyllaries, and a flower lacking all but two of its pappus bristles; and *Fleischmannia pycnocephala* (below), including a fertile branch, a leaf, an involucre, and a flower lacking all but two of its pappus bristles.


5.5mm
2.5

1.5
4.0

stripes; achenes 1.5-2.5 mm long, glabrous or sparsely short-pubescent on the ribs; $n = 10$, $2n = 20$.

Plants of moist or mesic habitats and probably closely associated with calcareous soils: deciduous woods, frequently burned pineland, bluffs, margins of ponds, creeks, and swamps, cedar glades, limestone ledges, prairies, old fields, and roadsides. Distributed mostly in isolated populations in South Carolina, Tennessee, Arkansas, Louisiana, eastern Oklahoma, Texas, and in Mexico, in the states of Nuevo Leon and Veracruz; also scattered southward through the Gulf states to central Florida and northward to southern Virginia, West Virginia, and the southern portions of Ohio, Indiana, Illinois, and Missouri (Figs. 1 & 2). Flowering mostly from September into early November; occasionally as early as late March and, in central Florida, as late as early December.

Plants of *Fleischmannia incarnata* can be mistaken for those of *F. pycnocephala* (Less.) King & Robinson (= *Eupatorium pycnocephalum* Less.), a species of South and Central America, which extends into the deserts of the southwestern United States. The latter species is distinguished by the following characters: corymbs dense with terminal peduncles only 1-3(-4) mm long, phyllaries broadly oblong-obtuse or sometimes acute, and corollas 1.5-2 mm long (Fig. 2). *Fleischmannia pycnocephala* belongs to the *F. microstemon* (= *Eupatorium microstemon*) species aggregate studied by Baker (1967).

Chromosome numbers were determined in three plants from Leon County, Florida. From a root tip of FPl, 20 somatic chromosomes were observed, agreeing with a count by Grant (1953) for this species. Ten meiotic bivalents were counted in TT4-10, and 10 meiotic bivalents plus two pairs of accessory chromosomes were seen in GC9-8. The accessory chromosomes were roughly half the size of those of the regular complement, and they tended to lie off the spindle during the first meiotic division. They were highly heterochromatic and appeared shiny when viewed with phase contrast optics during diakinesis and metaphase I.

Conoclinium coelestinum (L.) DC., Prod. 5: 135. 1836.

Eupatorium coelestinum L., Sp. Pl. 838. 1753.

Conoclinium dichotomum Chapman, Coult. Bot. Gaz. 3: 5. 1878.

Eupatorium coelestinum f. *illinoense* Benke, Rhodora 35: 46. 1933.

Eupatorium coelestinum f. *album* E. J. Alexander, Castanea 5: 93. 1940.

Plants perennial, rhizomatous; stems herbaceous, often purplish, erect to decumbent, occasionally rooting at the nodes, up to ca. 1.5 m long, somewhat glandular-punctate, glabrate to short-villous, on new growth commonly minutely and densely puberulent; leaves opposite, membranous, mostly narrowly deltoid, deltoid-ovate, or nearly lanceolate, the longest blades up to 3-13 cm long, densely glandular-punctate beneath, glabrous to puberulent or hispidulous, apices acute or obtuse, bases subcordate to broadly cuneate, sometimes slightly hastate, margins crenate or crenate-serrate, blades of the larger leaves 2-5 times longer than their petioles, the petioles and veins sometimes purplish; heads borne in compact corymbs and bearing 40-90 flowers on a distinctly conical receptacle; involucres of 3 or 4 imbricated series of 22-32 similar phyllaries: the phyllaries of the outer series shortest (1.5-2.5 mm long) and those of the inner series longest (3-5 mm long); phyllaries linear-acuminate with the ends inwardly curved, glabrous or strigose, eglandular to moderately glandular-punctate, especially near the base, purple-tipped, 2-nerved, often with a narrow purple strip between the nerves; corollas tubular, 2-3 mm long, the lobes purple, 4-8 times shorter than the tube, glandular-punctate beneath, the tubes white, sometimes with purple stripes, sparsely glandular; achenes 1-1.8 mm long, glabrous, often glandular; pappus of ca. 25 bristles; $n = 10$, $2n = 20$.

Plants mostly of moist, open or semi-shaded habitats: banks of streams, ponds, and springs, in wet woods, dry creek beds, swamps, marshes, bogs, and pine flatwoods, and along roadsides; less commonly in dry woods (e.g., oak-

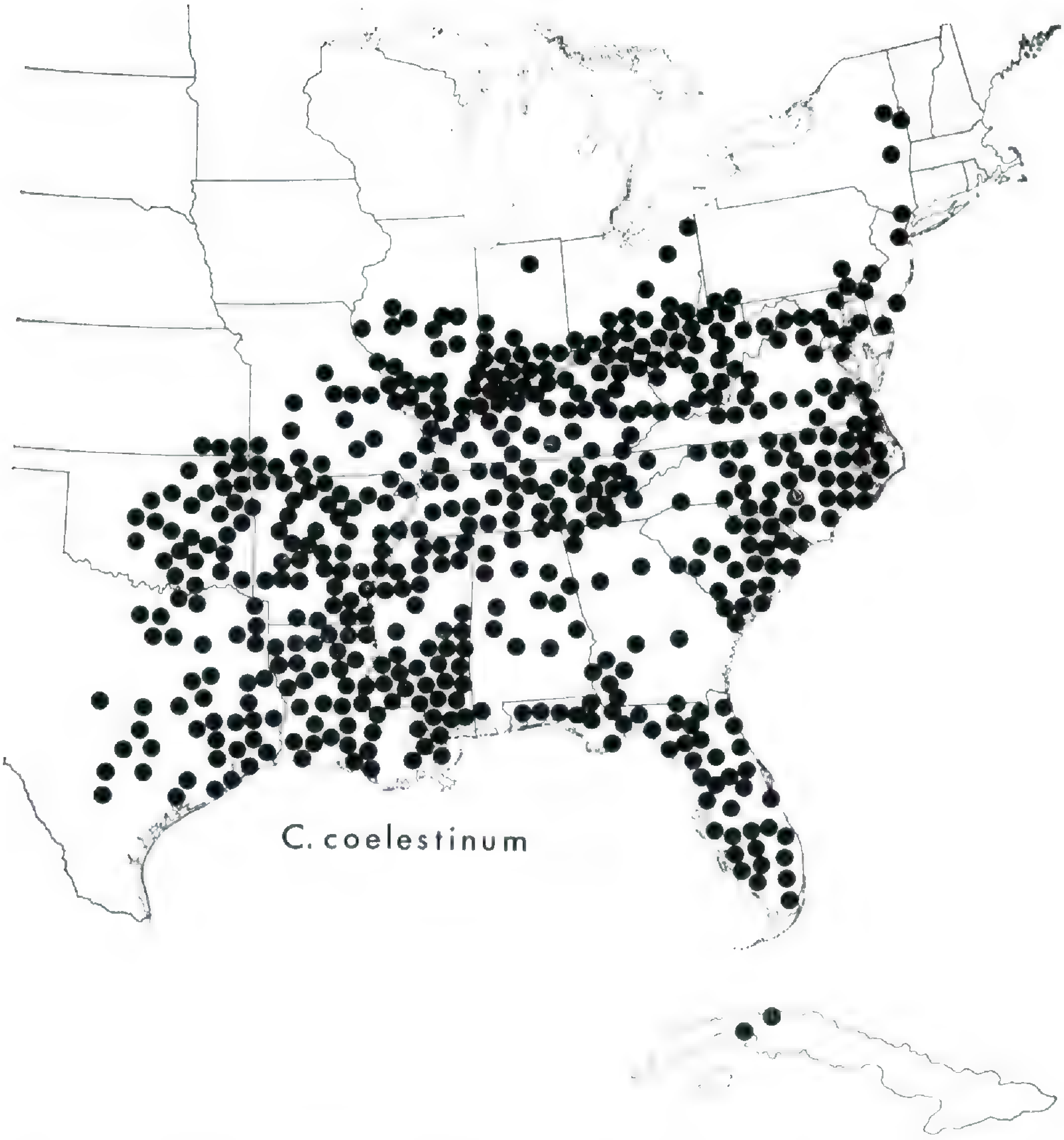


Figure 3. Distribution by county of *Conoclinium coelestinum.*

hickory, pine-oak-hickory, and upland, frequently burned pinelands) and old fields. Southern New Jersey and Pennsylvania west to central Missouri, southeastern Kansas, and eastern Oklahoma, south to Florida, eastern Texas, and Cuba (Figs. 3 & 4). Flowering mostly from September through October but sometimes as early as late April. Flowering later in southern regions and throughout the year in southern Florida.

Plants from peninsular Florida consistently have short

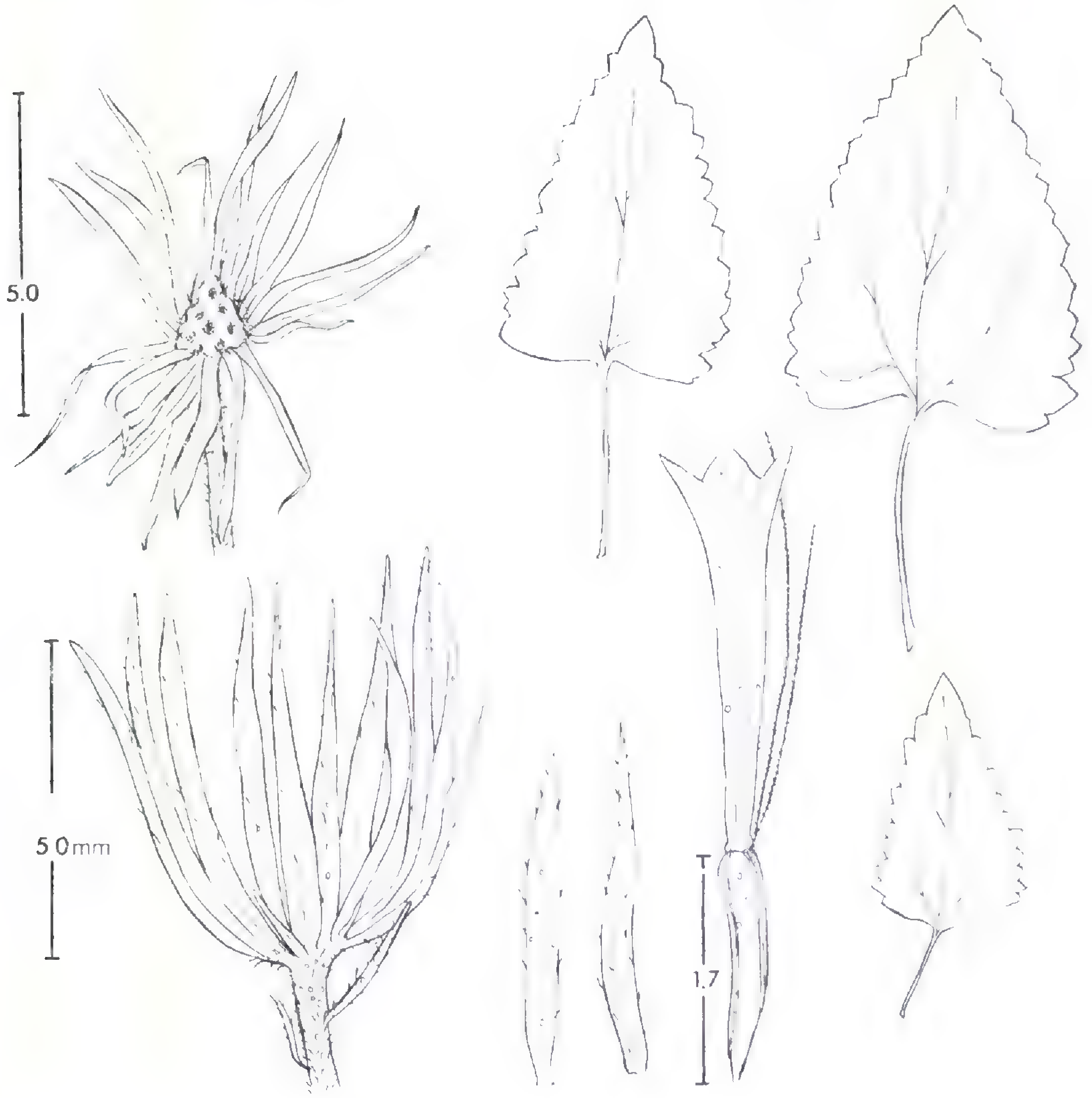


Figure 4. *Conoclinium coelestinum*, including two involucres, three leaves, two phyllaries, and one flower lacking all but two of its pappus bristles.

leaves and are identifiable as *Conoclinium dichotomum* Chapman; plants of this species were originally described as having leaves 1-1 1/2 inches long. The name *E. coelestinum* f. *illinoense* was applied to plants with rich red-purple flowers, and f. *album* to rare, white-flowered plants.

We counted 10 bivalents at meiosis in three plants from Leon County, Florida (GC10-9, TT17-2, FP3). Grant (1953) also reported 20 somatic chromosomes.

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NEW SPECIES OF CUSCUTA AND PHLOX FROM OKLAHOMA

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In southeastern McCurtain County, in a Coastal Plain flora which extends into the state along the Red River, there is a species of distinct-sepalled *Cuscuta* apparently resembling *C. compacta* Juss. However, the new species has flowers usually pedicellate, the pedicels up to 4 mm long, a bract at the base of the pedicel only; sepals are ovate-lanceolate to rather narrowly lanceolate, the tips attenuate, tending to become carinate; corolla lobes are deltoid-ovate, spreading at full anthesis, about equalling the tube; corolla deciduous from the mature fruit; infrastamineal scales ovate-oblong, fringed, the fringe extending about half way up the filaments, sometimes visible slightly above the bases of the corolla sinuses; fruits slightly depressed-globose.

C. compacta has flowers sessile, or essentially so, subtended by two or more ovate-orbicular bracts; sepals are ovate to ovate-orbicular, obtuse, resembling the bracts; corolla lobes much shorter than the tube; corolla investing the top of the mature fruit; infrastamineal scales oblongish, the fringes reaching the bases of the filaments; fruit ovoid to ovoid-globose.

The pedicellate condition might remind one of *C. cuspidata* Engelm., but that species has a much more open inflorescence, smaller flowers, usually 1 or 2 ovate, sometimes cuspidate bracts on each pedicel, sepals ovate-orbicular, corolla lobes oblong-ovate, shorter than the funnelform tube, corolla persistent on the subglobose fruit.

C. attenuata Waterfall, sp. nov., floribus densis, pedicellatis; pedicellis ad 4 mm longis; bracteis solitariis; sepalis distinctis vel subdistinctis, ovato-lanceolatis vel angusto-lanceolatis, apicibus attenuatis; corollo-lobis deltoidovatis, tubum aequantis; fructibus depresso-ovoideis.

Holotype: *Waterfall* 17157 (OKLA), Waterfall Creek, 8

miles south and 2 miles east of Idabel, McCurtain County, Oklahoma, Oct. 10, 1964. It was growing on *Iva ciliata*. Isotype (GH).

Another collection is *Waterfall* 17496 (OKLA), on *Iva ciliata*, edge of pond in Waterfall Creek, 7 miles south and 1.5 east of Idabel, McCurtain Co., Oct. 3, 1970.

The polysepalous condition and the dense aggregations of flowers would indicate *C. attenuata* as belonging to subsection *Lepidanche* Engelm. (Yuncker, 1965). However, the presence of a single bract at the base of the pedicel, and the depressed-globose capsule suggest the desirability of creating a new subsection for this new species.

The author has long been aware of an anomalous *Phlox* in southwestern Oklahoma, especially in the granitic areas extending west and northwest of the Wichita Mts proper, which are laregly in, and north of, the Wichita Mountains Wildlife Refuge in Comanche County. This is the taxon listed as "*Phlox* sp. ined." in my KEYS . . . (Waterfall 1969, and previous editions, 1962 and 1966).

This was treated by Wherry (1955) as *Phlox pilosa* L., subsp. *latisepala* Wherry (*P. aspera* E. Nels., 1899, non *P. aspera* Muhl., 1813). The differences in the next paragraph are shown largely by comparison with the holotype of *P. aspera* E. Nels., *Heller* 1641 (MO).

P. longipilosa differs most obviously from subsp. *latisepala* in having long, jointed hairs, 2-4 mm long, on the calyx where they are sometimes very abundant, on the stem, and often the leaves. The hairs of subsp. *latisepala* are mostly under 0.5 mm long. The sepals of *P. longipilosa* are 10-12 mm long, apically attenuate-awned, and often somewhat twisted; those of subsp. *latisepala* are 8-10 mm long. The new species has upper leaves alternate, sometimes as many as 7-8 being so; subsp. *latisepala* has them opposite, sometimes 1 or 2 being closely alternate. Fruits of *P. longipilosa* are 3-3.5 mm wide; those of subsp. *latisepala* are 2.5-3 mm wide.

It might be compared, in some respects, with *P. pilosa* var. *pilosa* which has many hairs 0.5-0.7 mm long, some-

times a few 1 mm long; the leaves are uncrowded, usually 5-9 pairs, the upper leaves normally opposite. *P. longipilosa* has leaves crowded, growing from 10-18 nodes.

Phlox longipilosa Waterfall, sp. nov. Planta erecta, 20-45 cm alta, perennis; caulibus pluribus; foliis congestis e 10-18 nodis, linearo-lanceolatis vel linearibus, integris, supernis alternatis, infernis oppositis; calicibus et caulibus, et interdum foliis, longipilosis; trichomatibus articulatis, 2-4 mm longis; calycibus ca 10-12 mm longis; fructibus 3-3.5 mm latis.

Holotype: *Waterfall* 13134 (OKLA) northern slopes of granite mountains south of Lake Altus, Kiowa County, May 29, 1957. Isotypes: (GH, OKL, others to be distributed).

Other collections seen: **Oklahoma**. COMANCHE CO.: *C. T. Eskew* 1714 along foot of hills and streams, Wichita National Forest, May 9, 1937 (OKL). KIOWA CO.: *Waterfall* 9449 (OKLA) northern slopes of granite mountains, south of Lake Altus, May 14, 1950; *Waterfall* 11985 (OKLA) slopes of granite mountains southwest of Lake Altus, June 4, 1954; *Milton Hopkins*, & *Aven* & *Ruth Nelson* 240 (OKL) among boulders on granite hill in Quartz Mt. State Park, Apr. 30, 1944. GREER CO.: *Waterfall* 7247 (OKLA) southern slopes of Granite Mountains, north of Granite, June 21, 1947; *Ruth Logan* 98 (OKLA) Granite Park, Granite, Apr. 27, 1952; *G. W. Stevens* 1013 (OKL, OKLA) on mountainside, Granite, June 17, 1913 .

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RELATIONSHIP OF HERACLEUM LANATUM MICHX. OF NORTH AMERICA TO H. SPHONDYLIUM OF EUROPE

R. K. Brummitt

The one species of *Heracleum* native to North America has generally been known as *H. lanatum* Michx. or sometimes by the invalid name *H. maximum* Bartr. It extends from Newfoundland and Labrador to Alaska and south to Georgia and California, and the name *H. lanatum* has also been applied to plants from eastern Asia. The European *H. sphondylium*, occasionally naturalised in North America, has been distinguished from the native plant mainly by its having pinnate, as distinct from ternate, leaves (see for examples Mathias & Constance 1945, Fernald 1950, Gleason 1953, Gleason & Cronquist 1963). However, in preparing an account of this genus for Flora Europaea (1968) I found it necessary to adopt a broad concept of the species *H. sphondylium* so as to include plants ranging from those with pinnate leaves through those with ternate leaves to others with simple leaves, and the status of the American *H. lanatum* is thus now called into question.

In order to comprehend the position of the American plant it is necessary to consider the pattern of variation of *H. sphondylium* in Europe, where the morphological range of variation of the species as now understood is remarkably wide. In the nineteenth century many species were described similar to *H. sphondylium* but differing in such characters as the segmentation, lobing and toothing of the leaves, the indumentum of various parts, the size and shape of the fruits and the colour of the flowers. A fairly average species concept in this group about the turn of the century is exemplified by Coste (1903) who recognised as species six such variants (excluding the very distinct *H. minimum* Lam.) from France alone. In the present century there has been an increasing awareness among European botanists that although extreme variants look very different they

are connected by intermediates and no clear-cut distinctions can be drawn between them. At the same time some variants do show a geographical correlation which may allow recognition of infraspecific taxa. The increasing tendency to 'lump' these variants may be traced through Briquet (1905) and (1924), Thellung (1924) and (1926) and Fournier (1946), all of whom give subspecific rank to major geographical variants. Others, however, have occasionally remained reluctant to adopt such a wide species concept.

My own examination of herbarium specimens and field populations certainly confirms that one cannot draw specific limits in this complex on the basis of leaf form. Typical *Heracleum sphondylium*, widespread and often abundant in north-west Europe, has most leaves pinnate with two or occasionally three pairs of lateral segments. Its juvenile leaves, however, are simple, and in mature plants there is a gradation from the pinnate leaves on the lower stem through ternate to reduced simple leaves below the inflorescence. Furthermore, in the British Isles many flowering populations include occasional plants in which even the largest leaves are only ternate and not pinnate. In the mountains of central and southern Europe many populations appear to be fairly constant in having ternate leaves, often occurring in more compact and dense stands, and are referred to subsp. *montanum* (Schleicher ex Gaudin) Briquet. In the Alpine valleys, however, where the species is often abundant, and in the Iberian peninsula, there is commonly a complete mixture of plants with pinnate leaves, ternate leaves, and all intermediate stages where the terminal segment is dissected to varying degrees. Such is the extent of these intermediate populations that one may question whether it is advisable to attempt to maintain two taxa at all, even at only subspecific level. On the higher mountains from the Pyrenees to the Balkan peninsula populations occur in which the leaves are simple, these plants being referred to subsp. *pyrenaicum* (Lam.) Bonnier & Layens, but again many intermediates connect these to plants with ternate leaves. Roughly one may think of the

species as showing a cline of variation from pinnate to simple leaves from lower to higher altitudes, but in the Italian Alps I have observed the whole range of leaf form within a distance of less than half a mile.

Examination of herbarium specimens of *H. lanatum* from North America shows that it is fairly constant in having ternate leaves but is indistinguishable in leaf form from European plants referred to *H. sphondylium* subsp. *montanum*. Seymour (1969) has recently quoted fruit characters as well as leaf form to separate the American plant from *H. sphondylium*, but in the wide range of the latter in Europe plants with fruit matching those of *H. lanatum* are commonly found. I can, in fact, find no character to distinguish the American plant from *H. sphondylium* subsp. *montanum* and am obliged to reduce the name *H. lanatum* to synonymy:

H. sphondylium L. subsp. **montanum** (Schleicher ex Gaudin) Briquet in Schinz & R. Keller, Fl. Schweiz. ed. 2, **1**: 372 (1905).

H. montanum Schleicher [Cat. Pl. Helv. ed. 4, 19 (1821) nom. nud.] ex Gaudin, Fl. Helv. 2: 319 (1828), basionym.

H. maximum Bartr., Trav. 344 (1791), nom. invalid.

H. lanatum Michx., Fl. Bor. Am. **1**: 166 (1803), synon. nov.

H. douglasii DC., Prodr. **4**: 193 (1830), synon. nov.

It may be appropriate here to recall the arguments for and against use of the name *H. maximum* Bartr. which is used in some current Floras. Adoption of this name was recommended by Fernald (1944) since it clearly ante-dated *H. lanatum* Michx., but this was soon refuted by Rickett (1944) who pointed out that Bartram had failed to consistently adopt the Linnaean binary system of nomenclature and that none of his names could therefore be considered validly published. In a foot-note to Rickett's paper Fernald gladly concurred with this opinion but, peculiarly, later (1950) stuck to using *H. maximum* Bartr. This has been followed by Seymour (1969) but is incorrect even if

one were to maintain the American plant as a species distinct from *H. sphondylium.*

It may be questioned whether *montanum* is the earliest and correct epithet for this taxon at subspecific rank, for Bisse (1963) has adopted the name *H. sphondylium* subsp. *elegans* (Crantz.) Arcangeli, with subsp. *montanum* as a synonym of this. The name *H. sphondylium* subsp. *elegans* was certainly published by Arcangeli in the second edition of his Compendio della Flora Italiana, p. 612 (1894), but he cited no authority after the epithet, a most unusual omission in this work. In the first edition (1882) he had recognised a species "*H. elegans* Willd., sp. 1, p. 2a, 1422" immediately before *H. sphondylium*, and this name does not appear in the second edition. Willdenow, however, referred back to *H. elegans* of Jacquin (1774), who in turn had taken up the epithet from Crantz (1769), who here published it as *H. protheiforme* "δ *Elegans* aut *Problematicum*" (the note following clearly indicating that he intended this to be a variety) but had earlier (1767) given it simply as "δ *Elegans*". The type of Crantz's name I take to be the plate, tab. 2, in his 1767 work, reproduced again in 1769, despite his mention of a still earlier figure by Jacquin dating from 1762. Crantz's plate shows a plant, said to be from Schneeberg in Austria, with three simple leaves (albeit divided almost to the base) and one ternate leaf, apparently a narrow-leaved variant intermediate between what I have above referred to as subsp. *pyrenaicum* and subsp. *montanum*, though certainly closer to the former. On the other hand the plant figured as *H. elegans* by Jacquin (1774) is different, the larger of the two leaves being ternate but tending towards pinnate, the smaller leaf being clearly ternate, the segments of both leaves being very narrow as is not infrequently found in several subspecies of *H. sphondylium.* Now it seems to me that the connection between Arcangeli's subsp. *elegans* of 1894 and Crantz's var. *elegans* of 1767-9 is too tenuous for them to be regarded as homotypic nomenclatural synonyms. Certainly the plants described by the two authors under the epithet *elegans* are

different, for Arcangeli's *elegans* of both 1882 and 1894 are said to have pinnatisect leaves and are presumably only the narrow-leaved variant of subsp. *sphondylium*. Because of the omission of any former authority by Arcangeli in 1894, coupled with the fact that his plant is apparently taxonomically different from any former *elegans*, I regard *H. sphondylium* subsp. *elegans* Arcangeli 1874 as a new name. In any case, it seems that neither Crantz's plant nor Arcangeli's is taxonomically the same as the ternate-leaved subsp. *montanum*, although the plant figured by Jacquin as *H. elegans* may be an abnormal form of this.

H. sphondylium now seems to be a polymorphic species distributed through most of the north-temperate region but showing its greatest variation in Europe (from where a fairly conservative nine subspecies are recognised in Flora Europaea). Subsp. *montanum* is the most widespread form of the species, extending across North America, Siberia (where it has been known as *H. dissectum* Ledeb.) and the mountains of central and southern Europe. In Europe it is morphologically and roughly eco-geographically intermediate between subsp. *sphondylium*, with which it merges very widely at lower altitudes, and subsp. *pyrenaicum* into which it intergrades at higher altitudes. The European plant introduced in North America is *H. sphondylium* subsp. *sphondylium*.

Plants from Japan and China which have been variously referred to *H. lanatum*, *H. moellendorfianum* Hance or *H. barbatum* Ledeb. seem also to be certainly referable to *H. sphondylium* in the broad sense, some of them probably to subsp. *montanum*, though others having pinnate leaves should presumably be excluded from this subspecies. Hiroe (1958) recognises from Asia, excluding Japan, *H. lantaum* with ternate leaves and *H. sphondylium* with pinnate leaves, which may correspond to subsp. *montanum* and subsp. *sphondylium* respectively. Hiroe & Constance (1958) refer all Japanese plants of this complex to *H. lanatum* but describe it as having leaves ternately, ternately-pinnately or quinately divided. As these authors point out, further

elucidation of the pattern of variation in this complex in Asia is required.

Postcript. In commenting above on usage of the name *Heracleum maximum* Bartram I accepted the view of Rickett that Bartram's binomials were not validly published because he did not consistently adopt binary nomenclature for species. While my article was in press a paper by Robert L. Wilbur, 'A reconsideration of Bartram's binomials', was published in *J. Elisha Mitchell Sci. Soc.*, 87(2): 56-73 (1971), putting forward again the view that Bartram's binomials should be accepted. Wilbur quotes an important paper by E. D. Merrill which I had overlooked, 'In defence of the validity of William Bartram's binomials', in *Bartonia*, 23: 10-35 (1945), where Merrill argues that out of 360 plant names used by Bartram all but one or perhaps two may be interpreted as binomials, even though many of these may have been followed by descriptive latin phrases separated only by a comma. This paper by Merrill may now be seen to explain the *volte face* of Fernald over usage of the name *Heracleum maximum* which I have commented on above, and justifies Seymour's adoption of the name in preference to *H. lanatum* Michx. After studying Wilbur's and Merrill's papers I am now convinced that Bartram's names should in general be accepted as validly published; in the case of *Heracleum maximum* the descriptive matter given by Bartram is so scant that it might be regarded as a *nomen subnudum*, but I would allow that it is just sufficient for validation of the name. This postscript does not, however, change my opinion that the correct name for the American plant is *H. sphondylium* subsp. *montanum*.

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THE HERBARIUM
ROYAL BOTANIC GARDENS
KEW
RICHMOND
SURREY, UNITED KINGDOM

ERRATA

p. 111, line 12 Elaphantopus should be Elephantopus

p. 251, et seq. page heading Hillquist should be Hellquist

p. 255, line 2 from bottom E. acicularis (l.) should be E. acicularis (L).

p. 255, line 12 *trivale* should be *triviale*

p. 256, line 2 from bottom Pontedaria should be Pontederia

p. 277, line 6 Focus should be Fucus

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